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Announcement

In June 1971 the Canadian Metric Commission was established by Order-in-Council to prepare an overall plan for metric conversion. Beginning in January 1977 we will convert to the International System of Units (SI) in the *Journal* and other publications of the Fisheries and Marine Service. This conversion to the metric system of measurements is to serve the best interests of readers and authors alike, since it is generally agreed that for scientific and technical work the International System of Units is superior to other systems, and this system is more widely accepted than any other as the common language in which scientific and technical data should be expressed. The National Standards of Canada publications, The International System of Units (SI), (CAN-3-001-01-73, CSA Z-234.2-1973) and the Metric Practice Guide (CAN-3-001-02-73, CSA Z-234.1-1973), available from the Canadian Standards Association, 178 Rexdale Blvd., Rexdale, Ontario, M9W 1R3, may be referred to for information and treatment of SI and its use.

Avis

La Commission canadienne du système métrique fut créée en juin 1971 par décret du conseil dans le but de préparer un programme global de conversion au système métrique. A compter de janvier 1977, le *Journal* et autres publications du Service des pêches et des sciences de la mer adopteront le Système international d'unités (SI). Cette conversion au système métrique est dans le meilleur intérêt tant des lecteurs que des auteurs, car il est généralement reconnu que le Système international d'unités est supérieur aux autres systèmes dans les travaux scientifiques et techniques, et que ce système est plus largement accepté que tout autre comme forme commune d'expression de données scientifiques et techniques. Pour renseignements sur le SI, son traitement et son usage, on pourra consulter les publications du Conseil canadien des normes: Système international d'unités (SI), (CAN-3-001-73, CSA Z-234.2-1973) et Guide pratique du système métrique (CAN-3-001-02-73, CSA Z-234.1-1973) que l'on peut se procurer en s'adressant à Association des normes canadiennes, 178 boul. Rexdale, Rexdale, Ontario, M9W 1R3.

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Effects of Sand Sedimentation on Colonization of Stream Insects[1]

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LUEDTKE, R. J., AND M. A. BRUSVEN. 1976. Effects of sand sedimentation on colonization of stream insects. J. Fish. Res. Board Can. 33: 1881–1886.

Driftnets, basket samplers, and artificial streams were used to investigate the influence of heavy sand accumulations on insect drift, colonization, and upstream movements in Emerald Creek, northern Idaho. Most riffle insects successfully passed through low-velocity, sandy reaches 80 m long. Upstream movements on sand were impeded by flows as low as 12 cm/s, except for the heavily cased caddisfly *Dicosmoecus* sp.

LUEDTKE, R. J., AND M. A. BRUSVEN. 1976. Effects of sand sedimentation on colonization of stream insects. J. Fish. Res. Board Can. 33: 1881–1886.

Nous avons utilisé des filets de dérive, des paniers d'échantillonnage et des cours d'eau artificiels dans nos recherches sur l'influence de fortes accumulations de sable sur la dérive, la colonisation et les mouvements en amont des insectes dans le ruisseau Emerald, Idaho septentrional. La plupart des insectes de radiers franchissent avec succès des étendues sablonneuses de faible vélocité de 80 m de longueur. Les mouvements en amont sur le sable sont entravés par des écoulements aussi lents que 12 cm/s, sauf ceux de l'éphémère *Dicosmoecus* sp., protégé par une lourde enveloppe.

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HEAVY sedimentation caused by commercial and private mining of garnets from Emerald Creek in northern Idaho is potentially detrimental to the benthic organisms and food chain relationships in the stream. Of greatest concern are long, sandy reaches formed during low, midsummer flows. These reaches serve as potential ecological blockages in the colonization cycle by impeding insect drift and upstream dispersion.

Insect drift is the major means of colonizing natural and altered streams (Leonard 1942; Müller 1954; Waters 1964). Distances insects drift are extremely variable, influenced by the insect species, substrate type, current velocity, and other stream characteristics (Elliott 1971a).

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Upstream migration by insects has been reported to be from 5 to 30% of downstream drift and could serve to colonize rehabilitated reaches of a stream (Bishop and Hynes 1969; Brusven 1970a; Elliott 1971b; and Hultin et al. 1969).

Field and laboratory dispersion studies were conducted to determine how benthic insects are affected by long sandy reaches in Emerald Creek. The studies were designed to obtain information on distance traveled by drifting and crawling insects, upstream dispersion, the capability of low water velocities to effectively aid insect movement for long distances, and the ecological impact of heavily sanded reaches on colonization.

Materials and Methods

Study Area

Emerald Creek is a major tributary of the St. Maries River in northern Idaho. It is a low-gradient stream through its intermediate and lower reaches, dropping 1.6 m/km. Stream width varies from 3.4 to 10.7 m. Average riffle depth is 5.1–15.2 cm; pools are 0.6–1.2 m deep during midsummer flows. The average summer discharge is 442 liters/s (Prather 1971). The upper and middle reaches of Emerald Creek and its tributaries have been extensively mined by rock hounds seeking gem quality garnets. The lower reach is influenced by a commercial dredge mining operation and has heavily sanded runs (mean particle size 1.27 mm) and pools.

Field Study

Basket samplers and driftnets were used concurrently to determine if riffle insects successfully passed through long, low-velocity sandy runs, and if so, by what means (i.e. drifting or crawling). A sandy run, approximately 80 m long, occurring between distinct riffles, was investigated. Nets, 30 × 60 cm with 0.8-mm pore size, were used to measure drift. Baskets (30 × 30 × 15 cm, made of 5.1 × 10.2 cm hardware cloth) filled with 12–15-cm rocks were used as colonization sites for drifting and crawling insects.

Single driftnets (nets A, B, and C) were positioned in center channel approximately 24 m apart in the sandy reach. A control net was placed in a riffle immediately upstream from the first test net (A). On three successive nights the control net and one test net were employed to sample insect drift. The lowermost net (C) was used on the first night and nets B and A during the next two nights, respectively. Drift results from the three test nets were compared with drift in the control net for the respective days. Drift was taken for a 10-h period starting before dark and ending after sunrise. Nets were emptied at 5-h intervals to avoid possible overloading by debris and insects. Volume of flow through each drift net was determined and insect drift enumerated as the number of insects per cubic meter of water.

Two basket samplers were placed in the center channel at each test and control driftnet site. These were positioned in the stream at the onset of the drift sampling period and emptied 24 h later. To prevent loss of insects during sampling, a net was placed immediately downstream from the basket to collect insects dislodged during basket removal. Rocks were emptied from the baskets and washed clean of insects.

Upstream dispersion was investigated in the field using an open-ended, linear channel (1.2 × 9.8 m) constructed of plywood boards and positioned in the thalweg of a sandy run. Water velocity in the channel was 21 cm/s and water depth 17.8 cm. Driftnets were positioned at the downstream end of the channel. Late-instar larvae of *Dicosmoecus* sp. and nymphs of *Pteronarcys californica* Newport and *Acroneuria* sp. were used as test specimens. Daytime tests were conducted between 1300 and 1600, night tests 1 h after sunset to 0100. Ten specimens of each species were used for each test (replicated 3 times). The insects were introduced into the middle of the channel and observed continuously for 15 min. A fluorescent tagging technique developed by Brusven (1970b) permitted visual observations of tagged insects at night.

Laboratory Study

In an attempt to better describe insect movement on sandy reaches, tests were conducted in a laboratory channel employing McLay's (1970) model to describe patterns of insect drift and settle-out.

$$N_x = N_o e^{-RX}$$

where: N_x = number of insects in the drift sampler,
N_o = initial number of drifting insects,
e = base of natural logarithms,
R = rate of return to the bottom,
X = distance upstream from the sampler (i.e., the origin of drifting insects).

Effect of different insect species, current velocity (12.2, 21.3 and 30.5 cm/s) and light conditions (light and dark) on R (rate of return to bottom) was investigated.

The laboratory stream consisted of two sections (2.4 and 3.1 m long, 25.4 cm wide and 20.5 cm high) connected by a flexible joint to permit slope adjustment. Both sections were of similar construction having a plywood base and 0.6-cm plexiglass sides. The channel was divided into eight, 60-cm test sections. A net was positioned at the outflow to collect test specimens drifting out of the channel. The water was 5–6 cm deep during the test; mean particle size of the sediment was 1.27 mm.

Four insect species, *Arcynopteryx* sp., *Brachycentrus* sp., *Ephemerella grandis* (Eaton) and *Pteronarcella badia* (Hagen) were used in laboratory tests. Test specimens were collected in the field and acclimated in a circular laboratory stream described by Brusven (1973). Twenty insects of a single species were introduced into the middle of the water column at the upstream end of the channel. Duration of each test was 15 min, after which the insects were re-

TABLE 1. Field drift analysis for number of species, total numbers of insects, and drift densities (number per cubic meter) for Emerald Creek in July and August 1972. Recorded values represent means for two, 5-h sampling periods.

Date	Net position	No. species	Total no.	Drift density ($No./m^3$)	Current velocity (cm/s)
July 7, 1972	Control	23	631	0.95	49.4
	C	16	158	0.95	12.5
July 8, 1972	Control	28	1076	1.35	63.4
	B	21	361	0.70	30.5
July 9, 1972	Control	26	645	0.75	60.1
	A	22	363	0.70	19.2
Aug. 17, 1972	Control	18	271	0.75	30.2
	C	9	39	0.50	6.4
Aug. 18, 1972	Control	18	314	0.85	31.1
	B	15	96	0.50	12.2
Aug. 19, 1972	Control	22	303	0.90	28.7
	A	15	85	0.45	7.0

covered and recorded from each 60-cm section of the stream and outflow net. Three replications were made for each species at each water velocity of 12.2, 21.3, and 30.5 cm/s under light and dark conditions.

Results and Discussion

DRIFT AND BASKET COLONIZATION STUDIES

Field drift and colonization results during July 1972 exhibited noticeable variability for the 3-day test period (Table 1). Numbers of species, total numbers of insects, and drift densities were approximately equal at test nets A and B. Net C yielded higher drift density but fewer species and total numbers. Increased drift at the control net on the second night is believed to have been influenced by a late-afternoon rain shower that caused increased flow. Similar conditions described by Anderson and Lehmkuhl (1968) caused increases in drift numbers. Basket sample counts at the driftnet sites indicated the control site increased during each successive sampling period while counts at test site B were substantially higher than those from sites A and C (Table 2).

The mayflies *E. hecuba* Eaton and *E. teresa* Traver and the beetle *Optioservus seriatus* LeConte were the most abundant species in both control and test driftnet samples during July; however, only *E. teresa* was abundant in basket samples (Table 3). The mayflies *Centroptilum* spp. A and B, *Epeorus albertae* (McDunnough) and *Baetis tricaudatus* Dodds, and the Chironomidae (Diptera) were the most common insects in basket samples, indicating colonization was not proportional to drift densities for these species. The standing crop in the sandy run was composed primarily of dipterans (Chironomidae and *Hexatoma* spp.) and the mayfly *Centroptilum* sp. A. Other species reported in Table 3 are common riffle inhabitants.

TABLE 2. Mean basket sample count from two baskets at each site for a number of species and total number of insects from Emerald Creek in July and August 1972.

Date	Basket position	No. species	Total no.
July 7, 1972	Control	13.0	44.0
	C	10.5	20.0
July 8, 1972	Control	11.0	50.5
	B	13.0	47.5
July 9, 1972	Control	13.0	65.5
	A	7.0	15.0
Aug. 17, 1972	Control	10.0	46.5
	C	9.0	31.0
Aug. 18, 1972	Control	9.0	72.0
	B	8.5	36.0
Aug. 19, 1972	Control	8.0	63.5
	A	8.0	26.0

August drift was much less variable than July drift. Drift at the control site was reasonably consistent during the test period (Table 1). Nets A and B had similar numbers of species and total numbers while net C had the fewest. Drift density was much less variable among the three test nets (Table 1). Basket colonization during August reflected fewer species than in July but slightly greater numbers (Table 2).

The mayfly *Centroptilum* sp. B, caddisfly *Brachycentrus* sp., and stonefly *Arcynopteryx* sp. were the most common insects in the August test and control drift samples (Table 3 and 4).

The dominant drift species (i.e. *Centroptilum* sp. B, *Arcynopteryx* sp. and *Brachycentrus* sp.) were prominent in basket samples at the control

TABLE 3. Percent composition of insects from July 1972 net (N) and basket (B) samples for selected species.

Insect		Net and basket position					
		A	Control	B	Control	C	Control
Coleoptera							
Optioservus	N	18	16	33	29	43	23
seriatus	B	—	1	0	0	0	3
Diptera							
Chironomidae	N	5	2	4	2	1	<1
	B	—	19	14	26	3	18
Simulium sp.	N	<1	<1	0	<1	0	0
	B	—	16	3	9	6	13
Ephemeroptera							
Baetis	N	8	4	5	3	4	3
tricaudatus	B	—	17	12	8	3	6
Centroptilum	N	1	<1	1	<1	<1	<1
sp. A	B	—	0	3	0	32	0
Centroptilum	N	4	4	1	1	2	3
sp. B	B	—	8	15	2	23	12
Ephemerella	N	30	35	26	26	16	27
hecuba	B	—	3	7	<1	3	0
E. flavilinea	N	2	2	2	4	2	6
	B	—	2	1	13	0	7
E. teresa	N	10	15	12	13	15	19
	B	—	1	5	10	6	9
Epeorus	N	2	3	2	3	3	3
albertae	B	—	12	8	11	6	9
Trichoptera							
Brachycentrus sp.	N	8	6	6	6	3	4
	B	—	6	5	7	3	9
Micrasema sp.	N	0	<1	0	0	1	0
	B	—	6	9	13	0	9

site. However, as in July, the dominant drift species was not the dominant insect from the respective test basket sample. *Centroptilum* sp. A and Chironomidae, common to the sandy run, were the most common insects in the three sets of test basket samples.

Drift and basket colonization results indicated appreciable downstream movement (drifting and crawling) by insects on a sandy substrate despite low current velocities. Most riffle drifting insects successfully moved through the test reach as evidenced by similar drift densities and species composition for the three test nets. The relative species composition appeared to be similar for both driftnet and basket samples from the test sites. However, dominant "drift" species were not the dominant "basket" species. Variability in colonization of the baskets probably reflects species-specific responses to the habitat afforded by the baskets, dominant species in the immediate area of the baskets, and mode of displacement i.e. passive or active, by drifting insects. Baskets were found to be most frequently colonized by insects that were either common to the immediate area of the basket (e.g. Chironomidae and *Centroptilum* sp. A at the test sites) or were strong swimming species (e.g., *Centroptilum* sp. B, *Baetis tricaudatus* and *E. albertae*). *Ephemerella hecuba* and *O. seriatus*, considered to be weak swimmers, were the dominant drift species in July but were not abundant in either control or test baskets. In contrast, August drift was partially dominated by actively swimming forms (e.g. *Centroptilum* sp. B and *Arcynopteryx* sp.) which were the principal species in control basket samples.

ARTIFICIAL STREAM STUDIES

Laboratory simulation studies provided additional insight into insect movement and "return to substrate rates" (R) on sand substrates. Highest R values for the mayfly *E. grandis* and the stonefly *P. badia* (Hagen) were under lighted conditions and the low current velocity of 12.2 cm/s (Table 5). The stonefly *Arcynopteryx* sp. and the caddisfly *Brachycentrus* sp. exhibited highest R values under lighted conditions and higher current velocity (21.3 and 30.5 cm/s).

TABLE 4. Percent composition of insects from August 1972 net (N) and basket (B) samples for selected species.

Insect		Net and basket position					
		A	Control	B	Control	C	Control
Coleoptera							
Optioservus seriatus	N	4	2	3	1	6	1
	B	0	3	0	1	0	0
Diptera							
Chironomidae	N	7	4	9	3	9	5
	B	14	2	33	6	33	8
Hexatoma sp.	N	0	0	0	0	0	0
	B	0	0	1	0	8	0
Ephemeroptera							
Baetis tricaudatus	N	4	2	3	2	1	5
	B	3	3	4	3	1	4
Centroptilum sp. A	N	3	<1	4	<1	10	1
	B	22	1	6	1	32	0
Centroptilum sp. B	N	25	14	30	22	17	18
	B	15	51	25	46	10	43
Hemiptera							
Sigara sp.	N	3	1	3	<1	0	1
	B	4	0	0	0	0	0
Plecoptera							
Alloperla sp.	N	4	1	8	2	9	2
	B	0	1	0	0	0	0
Arcynopteryx sp.	N	15	11	7	9	14	10
	B	13	6	7	3	6	8
Pteronarcella badia	N	2	6	6	7	4	6
	B	0	5	0	<1	0	1
Trichoptera							
Brachycentrus sp.	N	22	51	18	45	13	44
	B	3	15	18	32	3	29
Hydropsyche sp.	N	2	2	2	2	5	1
	B	0	4	2	4	0	1

Return to substrate rates for all test species except *P. badia* were distinctly lower under dark conditions. Values of R for dead insects were nearly zero for all test species (Table 5).

Different species displayed different mechanisms for drifting. *Ephemerella grandis* folded its legs to initiate drift, then extended them to engage the substrate and stop. *Pteronarcella badia* displayed a "tuck and roll" behavior to begin drift. *Arcynopteryx* sp. initiated drift by releasing the substrate and holding its legs in an extended, fixed position.

From these results we contend that "return to substrate" by the species studied was "active" and not "passive." Both live and dead specimens made numerous contacts with the substrate as they drifted. Difference in R values for live and dead specimens indicated that the return to substrate values was largely dependent on the physical activity of the insects e.g. swimming, grasping, and gliding behavior.

We initially hypothesized that the rate of return to substrate on sand would be lower than on pebble or cobble substrates. Values we obtained, however, are comparable to those reported by Elliott (1971a) from a small cobble stream. Relatively high rates in this study can be partially attributed to the shallow water column (5–6 cm) and short drift distance of the artificial channel.

UPSTREAM DISPERSION

Upstream dispersion studies conducted in the field revealed that the stoneflies *Pteronarcys californica* and *Acroneuria* sp. did not move upstream on a sand substrate with low current velocities of 21 cm/s. After several unsuccessful attempts, most specimens actively swam downstream, usually reaching the end of the channel (4.9 m) within 2–3 min. In contrast, the heavy-cased caddisfly *Dicosmoecus* sp. moved in a random manner (i.e. upstream, downstream, and

TABLE 5. Return to the substrate rates (R) for living and dead *Ephemerella grandis*, *Arcynopteryx* sp., *Brachycentrus* sp., and *Pteronarcella badia* in a laboratory stream at three water velocities in light and dark conditions.

Water velocity (*cm/s*)	*E. grandis*		*Arcynopteryx* sp.		*Brachycentrus* sp.		*P. badia*	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark
			Settle-out rates (R) for live insects					
12.2	1.16	0.96	1.08	0.81	0.45	0.21	0.59	0.49
21.3	0.68	0.61	1.02	1.08	0.60	0.44	0.43	0.46
30.5	0.41	0.27	1.13	0.78	0.59	0.16	0.22	0.26
			Settle-out rates (R) for dead insects					
12.2	0.05	—	0.41	—	0.07	—	0.06	—
21.3	0.03	—	0.04	—	0.00	—	0.00	—
30.5	0.00	—	0.07	—	0.00	—	0.01	—

cross-channel). Many were noted moving upstream, often reaching the upper end of the channel in 5–10 min. This behavior suggests that this species can successfully colonize an upstream habitat when subjected to an unfavorable substrate at a lower reach. Tests conducted at night produced essentially the same results as those conducted in daylight for the species studied.

Limited upstream movement was also noted in laboratory streams. *Ephemerella grandis*, *Brachycentrus* sp. and *Pteronarcella badia* showed no tendency to move upstream on sand substrates (mean particle size 1.27 mm) at current velocities of 12.2, 21.3 and 30.5 cm/s. Some stonefly nymphs of *Arcynopteryx* sp. were successful at moving upstream; however, most showed a net movement downstream.

Results from these field and laboratory studies indicated that many common riffle insects are unable to move upstream on sand substrates. Pebble and cobble may be necessary for upstream by most insects even at low current velocities. A layer of water with zero velocity has been shown to exist at rock–water interfaces (Ambühl 1959). McClelland (1972) reported that many insects apparently live in this zone and do not experience the direct forces of current. This zone is probably thin on fine, loosely compacted sediments. The combination of exposure to current and instability of sand grains is believed responsible for restricting upstream movement by insects on sandy reaches such as occur in Emerald Creek and other streams having heavy sand deposition.

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Influence of Temperature and Wind on the Survival of Early Stages of Yellow Perch, *Perca flavescens*[1]

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Survival from the egg to larval stage was estimated for the 1969–75 year-classes of yellow perch, *Perca flavescens*, in Oneida Lake. Egg production was determined from mark-and-recapture estimates of adult stock and measurements of fecundity, and abundance of the resulting cohort was estimated from annual larval surveys. Early survival, which varied from 1.6 to 18.4% was correlated positively with temperature and negatively with wind. Two variables, mean daily air temperature during the 3 wk prior to the date the larvae attained a mean length of 8 mm and mean daily wind velocity for 4 wk prior to this date, accounted for 87% of the variability in survival of perch. Physical destruction and movement of eggs by high winds and greater mortality of prolarvae caused by low temperature could account for the differences in survival between years, but do not appear severe enough to account for the 80+% base mortality that occurred in all years. The low year-to-year variation in survival suggests that temperature and wind influenced year-class size through a complex of many relatively minor mortality factors, rather than through one catastrophic event.

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Nous avons estimé la survie, de l'œuf au stade larvaire, des classes d'âge de 1969–75 de la perchaude, *Perca flavescens*, du lac Oneida. Des estimations du stock adulte par marquage et recapture et des mesures de fécondité ont servi à déterminer la production d'œufs, alors que des recensements annuels des larves ont fourni une estimation de l'abondance de la cohorte issue de ces œufs. Nous avons trouvé une corrélation positive entre la survie du début, variant de 1.6 à 18.4%, et la température, et une corrélation négative avec le vent. Deux variables, la température moyenne quotidienne de l'air durant les 3 semaines précédant la date à laquelle les larves atteignent une longueur moyenne de 8 mm et la vitesse moyenne quotidienne du vent durant les 4 semaines précédant cette date, sont responsables de 87% de la variabilité dans la survie de la perchaude. La destruction physique et le déplacement des œufs causés par de grands vents, de même qu'une plus forte mortalité au stade prélarvaire causée par une basse température peuvent expliquer les différences dans la survie d'une année ça l'autre, mais ne semblent pas suffisamment importantes pour expliquer une mortalité de base de 80+% qui se produit tous les ans. La faible variation dans la survie d'une année à l'autre donne à croire que la température et le vent agissent sur la taille des classes d'âge par l'intermédiaire d'un complexe de plusieurs facteurs de mortalité relativement mineurs plutôt que par un événement catastrophique.

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POPULATIONS of yellow perch, *Perca flavescens*, often exhibit large fluctuations in year-class strength (Doan 1942; el-Zarka 1959; Heyerdahl and Smith 1971; Jobes 1952). Variation in year-class abundance is frequently attributed to direct or indirect effects of meteorological or hydrographic conditions on survival during early stages of development (Jobes 1952; Pycha and Smith 1955). However, efforts to identify variables affecting early survival by correlating environmental factors in early life with relative size of yellow perch year-classes recruited to the fishery have been unsuccessful (Doan 1942; el-Zarka 1959; Heyerdahl and Smith 1971; Jobes 1952), and difficulties in estimating early survival have discouraged more critical field studies of factors governing survival. Since the yellow perch is an important forage and game species in many northern lakes and since the consistency of the relative rankings of year-class abundance in Oneida Lake at several stages during the latter part of the first

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summer of life (Forney 1971) suggested that factors influencing mortality very early in life were most critical in determining strength of the year-class at the end of the 1st yr, this study was designed to examine the relation between survival and temperature and wind during the egg and prolarval stages with a view to determining when the bulk of mortality occurs.

Materials and Methods

Factors contributing to differences in cohort abundance at the beginning of the pelagic stage were examined by estimating annual egg production and survival from the egg to larval stage. Egg production was determined from mark-and-recapture estimates of adult stock and measurements of fecundity. Abundance of the resulting cohort was determined by annual larval surveys.

Egg Production

In alternate years from 1969 through 1975, the population of mature yellow perch in April was estimated with Bailey's modification of the Petersen method (Ricker 1958, p. 84) by finclipping 45–70,000 perch taken in trapnets and recapturing fish primarily in gillnets and trawls. Separate estimates were made for each age group except that fish age VIII and older were combined. Assuming mortality was constant, number of yellow perch in each age group in 1969, 1971, and 1973 was projected forward to estimate the number of each age in the intervening years (1970, 1972, and 1974) by using an annual survival rate which equaled the square root of the empirical biennial survival estimate. (The assumption of constant mortality was justified by the uniformity of the biennial survivals.) One exception was that the number of age III fish in intervening years (1970, 1972, and 1974) was projected backward from age IV using the concurrent annual survival rate of the preceding year-class.

Fecundity of age III and older perch was determined from a regression of number of eggs on length derived from counts of eggs in ovaries of 117 fish collected in 1968, 1969, and 1975. The regression is: $\log_{10}$ fecundity = 2.9396 + 0.0066 total length in millimeters. Based on the mean length of females in each age group, a mean fecundity was predicted from the regression and multiplied by the estimated number of females of that age. For each year, these products were totaled for all ages to give egg potential. Sex ratio for all years was assumed to be 1:1, because the sex ratio of 9,927 perch examined in 1958–73 was 48.7% females. Percentage of females ranged between 45.4 and 52.6 in 15 of the 16 yr. All female perch age IV and older were mature. For fish of age III, the estimated number of females was adjusted by a factor of .723, since only 72.3% of 481 age III females examined in 1969, 1970, and 1973 were sexually mature. Mean lengths of female yellow perch during the spawning season were taken from fish of various ages captured in gillnets during the June following spawning. With the exception of age III, the fish had not begun to grow by June. This slight bias in the one age-group was ignored since, except for 1973, the contribution of age III fish to the total egg potential was relatively small.

Larval Abundance

After eggs hatched, density of larvae was estimated from the catch and volume of water strained by high-speed samplers. A grid pattern was used to choose 42–54 sampling stations at random within 4–6 strata based on catches in 1965–68 (Noble 1968). Strata were designed so that effort was concentrated in areas of highest larval density. Depending on the time of the survey, the strata encompassed several areas of the lake (split along both axes) between the surface and 2.7 m or between the 2.7 and 5.5 m contours. Few larvae were found below 5.5 m. At each station, four samplers and a flowmeter were towed at random depths and parallel to a bottom contour for 5–7½ min at a speed of 3.6 m/s. Catches at each site were pooled and the total population of larvae was determined from the mean density per liter and volume of the lake to a depth of 5.5 m (971×10^8 m^3). Ninety-five percent confidence intervals around the estimates were equal to $\pm 2\ s_{\bar{c}}$, where $\bar{c}$ is the mean catch per volume strained and $s_{\bar{c}}$ is the standard error. More complete descriptions of the gear and sampling and statistical techniques are given by Noble (1968) and Forney (1975).

Abundance was estimated twice, once near the beginning and again near the end of the pelagic stage. Catches in the later survey were corrected for avoidance of samplers by larvae (Noble 1970). Linear regressions were fitted to the natural logarithms of mean catch per 10^4 liters on both mean total length in millimeters and time in days. Regressions were used to estimate density of larvae and the day on which cohorts reached a mean length of 8 mm. Larvae were defined as perch with a mean length of 8 mm or greater. Smaller fish were prolarvae.

Additional estimates of prolarval populations were made during the period of hatching in 1974 to describe changes in length and abundance during the time of recruitment. These estimates were derived from the catch of perch in a survey designed to estimate abundance of larval walleyes, *Stizostedion vitreum vitreum* (Forney 1975) and two extra series of catches made at 30 and 35 sites prior to and following the walleye series. Detailed length frequencies for these three series were based on measurements of 2,400 larvae.

Temperature and Wind

Water temperatures recorded by a thermograph at 2 m were available for the 3 wk preceding the day on which the population reached a mean total length of 8 mm. Since Oneida Lake does not stratify thermally before June, the measurement at 2 m should be typical of conditions from 0 to 5.5 m. Warming

TABLE 1. Estimated number of mature yellow perch (*Perca flavescens*) and mean total length of females (millimeters), by age-group, in Oneida Lake, 1969–75; 95% confidence intervals in parentheses.

Age		1969	1970	1971	1972	1973	1974	1975
III	Number	453,000 (256,000–650,000)	1,209,000	217,000 (87,000–347,000)	203,000	2,837,000 (2,301,000–3,372,000)	178,000	19,000 (7,000–31,000)
	Length	217.2	219.8	228.6	229.0	224.2	219.2	229.1
IV	Number	129,000 (70,000–187,000)	394,000	1,051,000 (827,000–1,275,000)	202,000	62,000 (16,000–108,000)	1,897,000	119,000 (58,000–179,000)
	Length	237.0	247.0	251.2	256.2	254.5	253.1	247.9
V	Number	1,167,000 (949,000–1,384,000)	107,000	342,000 (254,000–430,000)	654,000	189,000 (108,000–270,000)	57,000	1,269,000 (1,036,000–1,503,000)
	Length	255.5	259.8	265.7	264.1	260.3	267.4	264.3
VI	Number	368,000 (209,000–528,000)	833,000	88,000 (50,000–125,000)	251,000	407,000 (306,000–507,000)	180,000	52,000 (13,000–90,000)
	Length	271.0	267.2	266.7	271.5	277.5	276.1	271.5
VII	Number	366,000 (200,000–533,000)	114,000	595,000 (437,000–753,000)	52,000	184,000 (108,000–259,000)	164,000	172,000 (96,000–247,000)
	Length	279.4	278.3	274.2	287.3	281.6	281.3	281.9
VII+	Number	89,000 (17,000–161,000)	113,000	79,000 (15,000–143,000)	349,000	263,000 (163,000–362,000)	180,000	139,000 (63,000–215,000)
	Length	287.5	285.8	291.2	287.1	281.9	292.1	291.2
Total	Number	2,695,000 (2,307,000–3,084,000)	2,770,000	2,384,000 (2,072,000–2,697,000)	1,711,000	4,013,000 (3,502,000–4,524,000)	2,656,000	1,803,000 (1,530,000–2,075,000)

TABLE 2. Number of adult yellow perch, eggs, and larvae produced, and percent survival during the egg and prolarval stages, 1969–75; 95% confidence intervals in parentheses.

Year	No. adult perch (*millions*)	No. eggs (*billions*)	No. larvae (*billions*)	% Survival (*8-mm egg*)
1969	2.70	54.4	3.18 (1.78–4.58)	5.9
1970	2.77	48.5	4.36 (3.64–5.08)	9.0
1971	2.38	53.0	4.45 (3.67–5.23)	8.4
1972	1.71	42.4	3.25 (1.93–4.57)	7.7
1973	4.01	58.3	0.95 (0.62–1.28)	1.6
1974	2.66	58.4	1.61 (0.76–2.46)	2.8
1975	1.80	45.0	8.30 (2.22–12.77)	18.4

rate was defined as the slope of the regression fit to the daily water temperatures. Data on air temperatures for the same 3-wk period were provided by the National Weather Service at Hancock Airport (19 km from Oneida Lake). Mean and maximum wind velocities per day were compiled from the same source for the 4 wk preceding the date of attainment of a mean length of 8 mm.

Results

DEVELOPMENT OF COHORTS

Annual egg production was relatively stable considering that adult stock varied 2.3-fold (95% confidence limits averaged ±13.8%; Table 1). Of the estimated 39–55 billion viable eggs spawned, 0.95–8.30 billion perch survived to the larval stage (95% confidence limits averaged ±39.5%; Table 2). Number of larvae was not closely related to egg production or adult stock. A ninefold variation in size of cohorts at the larval stage was generated primarily by mortality between spawning and the time the entire year-class was pelagic. Survival averaged 7.7% but losses were much lower in 1975 when almost 20% survived and much higher in 1973 and 1974 when less than 3% of the perch survived the 3–4-wk period between spawning and recruitment to the larval stage (Table 2).

Hatching and Recruitment of Larvae

Prolarval perch populations were estimated at intervals during the period eggs were hatching in 1967 (Noble 1968) and in 1974 (Fig. 1). Density of prolarvae in 1967 consistently increased from the first survey when perch averaged 6.3 mm until hatching was complete when the cohort averaged 8.1 mm total length. In 1974, the increase in density of larvae was more abrupt and little change in density was detected after the population attained a mean length of 6.8 mm on 20 May. In general rate of population increase was apparently declining by the time the fish averaged 7.0 mm.

Length frequencies of the populations in 1974 indicated that hatching occurred mainly during a 2-wk period (Fig. 2). Since maximum size of newly hatched prolarvae was 6.2 mm in aquaria and growth rate averaged 0.1 mm per day (M. D. Clady unpublished data), much of the population present on May 9 had hatched several days before. At least a small portion of the population on May 20 was recently hatched prolarvae less than 6 mm (Fig. 2), but hatching appeared to be largely completed 5 days before the population attained a mean length of 8 mm. (Only two sac fry were seen in samples taken in the survey of May 23–26 when the mean total length was near 8 mm.)

The great majority of perch are probably still in the egg stage during the 4th wk prior to attainment of a mean length of 8 mm, but during the week immediately before attainment of 8 mm, virtually all perch are prolarvae or larvae. During the intervening 2 wk, large numbers of eggs and prolarvae are present in Oneida Lake.

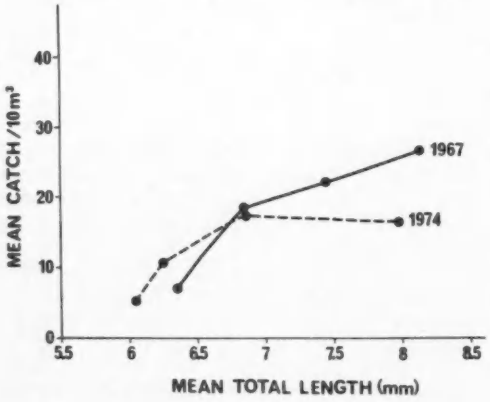

Fig. 1. Abundance of yellow perch (*Perca flavescens*) prolarvae in relation to their mean total length for the years 1967 (Noble 1968) and 1974.

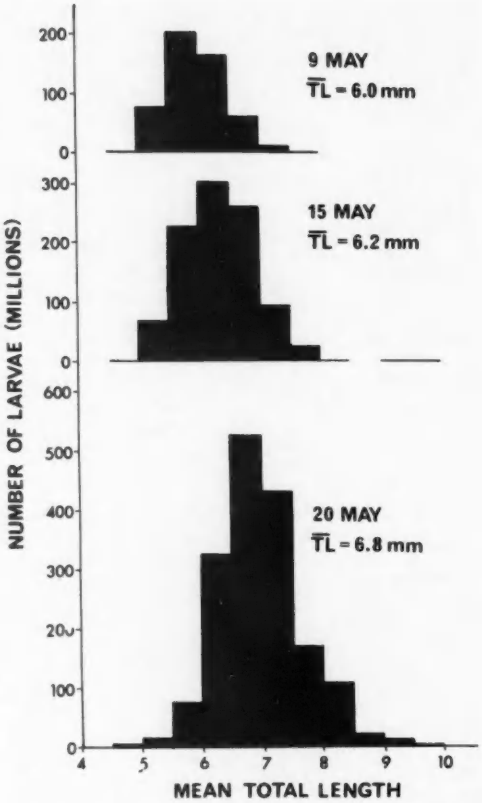

Fig. 2. Length-frequency distributions of populations of yellow perch prolarvae, May 1974.

Relation of Temperature to Survival

Perch spawn when water temperatures are 7–11 C. Water temperatures during the 3 wk preceding the date on which the cohort attained a mean length of 8 mm increased from 8–10 C when most perch were embryos to 12–19 C when most were prolarvae (Fig. 3). Annual mean temperatures during the period fell within the narrow range of 11.0–12.5 C (Table 3). Survival between spawning and 8 mm was higher in years when mean temperatures were higher ($r_s = 0.75$; Siegel 1956).

Examination of temperature trends revealed marked fluctuations which might be related to year-class survival (Fig. 3). Most eggs generally hatched 7–15 days before cohorts attained a

TABLE 3. Survival of yellow perch eggs and prolarvae, the date of recruitment of larvae to the pelagic stage, the mean daily water temperature,[a] the mean daily air temperature,[b] the mean daily wind velocity,[c] and the mean daily maximum wind velocity,[d] 1969–75; $*P < 0.05$, $**P < 0.01$.

Year	% survival (8-*mm egg*)	Date (8 *mm TL*)	Water temp (*C*)	Air temp (*C*)	Mean wind (*m/s*)	Max wind (*m/s*)
1969	5.9	May 24	11.4	12.6	3.8	8.5
1970	9.0	May 21	12.5	14.0	4.1	7.6
1971	8.4	June 1	11.8	14.6	3.9	7.2
1972	7.7	May 28	12.1	14.2	3.2	6.7
1973	1.6	May 25	11.0	10.6	4.2	7.6
1974	2.8	May 25	11.2	12.4	4.7	9.9
1975	18.4	May 24	11.5	16.4	3.6	7.1
r_s			.75*	.89**	−0.61	−0.54

[a]At a depth of 2 m for 3 wk preceding this date.
[b]For the preceding 3 wk.
[c]For the preceding 4 wk.
[d]For the preceding 4 wk.

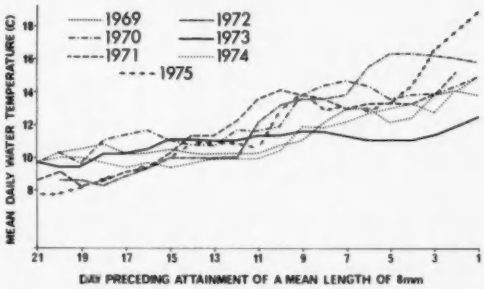

FIG. 3. Mean daily water temperature (C) at 2 m during the 3 wk preceding attainment of a mean total length of 8 mm, 1969–75.

mean length of 8 mm. Continuous records of temperature were not obtained during early egg stages (more than 21 days before attainment of a mean length of 8 mm) but apparently exposure of eggs to relatively low temperatures during late stages of embryonic development had little adverse effect since water temperatures in 1971, 1972, and 1975 were initially the lowest (below 9 C) and survivals of the three cohorts were all above 7.7%. Temperature diverged greatly during the latter 12 days of the period, when most fish were probably in the prolarval stage. Low survival (1.6–5.9%) occurred in 1969, 1973, and 1974 when temperatures remained between 11 and 14 C. High survival (7.7–18.4%) occurred in 1971, 1972, and 1975 when temperatures rose rapidly to between 16 and 19 C. The year 1970 was intermediate, with water warming quickly between 11 and 14 C but not changing thereafter. Exposure of prolarvae to temperatures near 10 C, as most likely occurred in 1969, 1973, and 1974, appeared to adversely affect survival. Warming rates throughout the 3-wk period, 0.37, 0.44, 0.64, 0.89, 0.19, 0.46, and 0.50 C/day for 1969–75, respectively, were not correlated as strongly with survival ($r_s = 0.50$) as were mean water temperatures.

RELATION OF SURVIVAL TO METEOROLOGICAL FACTORS

Lake temperatures are governed by meteorological conditions and close relationships between air and water temperatures are documented for Oneida (Jacobsen and Bachman 1974) and other lakes (Doan 1942; el-Zarka 1959; Fry and Watt 1957; Jacobsen and Bachman 1974). Mean daily air temperatures during the 3 wk preceding the time perch cohorts attained a mean length of 8 mm were correlated with estimates of early survival (Table 3). The positive relation ($r_s = 0.89$) between air temperature and survival is similar to the relation between water temperatures and survival. Slopes of regressions fitted to air and water temperature vs. survival (Fig. 4) are different however, probably reflecting the expected lag in response of water temperatures to rising air temperatures in the spring. This lag was reflected most dramatically in the mean temperatures for 1975 (Table 3).

Weather systems which contributed to above average air temperatures in May were associated with below average wind velocities (Table 3). Survival of perch was negatively related to mean daily wind velocity ($r_s = -0.61$) with a somewhat lower correlation ($r_s = -0.54$) with mean daily maximum wind velocities during a 4-wk

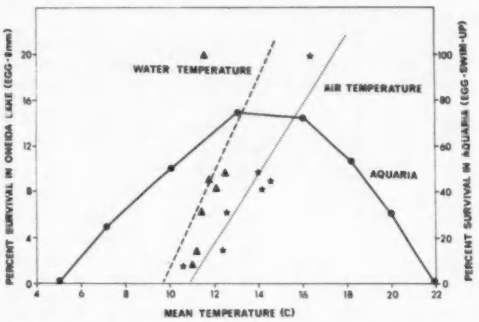

FIG. 4. Regressions of mean air and water temperatures (C) for the 3 wk before the cohort became pelagic on survival of yellow perch from the egg to a mean total length of 8 mm in Oneida Lake, 1969–75, and the relation between mean water temperatures (C) during incubation and survival of yellow perch from the egg to larval swim-up in aquaria (Hokanson and Kleiner 1974).

period prior to the time perch attained a mean length of 8 mm. Two variables, mean wind velocity and mean daily air temperature, account for about 87% ($R^2 = 0.87$) of the variability in perch survival.

Discussion

Egg production in 1969–75 was relatively stable despite modest fluctuations in adult stock and wide variation in abundance of year-classes. The multi-age character of the adult stock and the fairly low and constant mortality experienced by adult perch contributed to this stability. Presence of large numbers of older, more fecund perch in the population minimized the effect of differences in numerical size of year-classes recruited to the adult population during the period.

Examination of the ovaries of several thousand perch in spring and early summer over all years suggests eggs were seldom retained, and eggs produced were spawned under natural conditions present during this study. Abortion or incomplete fertilization of eggs is apparently uncommon. Only 3 of 130 egg masses collected in 1968–69 contained large numbers of dead eggs (J. Forney and R. Noble unpublished data). Excluding the three egg masses with mostly dead eggs, over 95% of the eggs collected in 1968–69 were viable. Possibly abortion of eggs was more common in years when temperatures were exceptionally low, as in 1973–74, but egg masses taken incidentally in trawls during April and May were usually viable.

The high viability of eggs found in Oneida Lake in 1968 and 1969 when water temperatures during late incubation varied between 8 and 12 C is consistent with the findings of Hokanson and Kleiner (1974). They found that mortality of embryos in aquaria generally exceeded 20% only when eggs were incubated at extremes of temperature below 8 C and above 20 C. Since water temperatures in Oneida Lake approached 8 C only during early stages of incubation which are most tolerant to low temperatures, eggs were incubated at temperatures that generally favored a high survival rate until swim-up.

The close relation between survival and temperature and large variation in survival over a narrow temperature range is difficult to reconcile with results of laboratory studies by Hokanson and Kleiner (1974), probably because the period examined was somewhat different. According to their findings, survival of yellow perch embryos exposed to constant temperatures of 5.0–22.1 C showed a parabolic relation to temperature and optimum survival to swim-up occurred between 13 and 16 C. Survival increased from 24.5% at 7.1 C to 75% at 13.1 C (Fig. 4). Survival of perch in Oneida Lake exposed to a similar range of temperature was a magnitude lower and more variable. However, eggs and larvae in the lake were exposed to a fluctuating temperature regime. Temperature changes can reduce or enhance survival depending on the tolerance limits of respective life stages and the position or level of the changing temperatures within its tolerance zone.

Although the causal relation between temperature and survival is obscure, air temperature or factors associated with temperature were also instrumental in determining abundance of young-of-the-year in years prior to 1969. Mean catches of yellow perch fingerlings in trawls from mid-August to mid-September of 1959–67 (Forney 1971, table 5) were correlated ($r_s = 0.74$; $P < 0.05$) with mean air temperatures from May 5 to 25, a period which approximates the 3 wk prior to attainment of 8 mm in 1969–75. (Mean temperatures were 14.8, 15.2, 14.8, 16.8, 12.4, 18.2, 15.1, 10.9, and 9.0 C for 1959–67, respectively.)

Although moderate winds are probably necessary for normal development of yellow perch eggs (proper currents provide circulation for eggs in the accordian-like egg masses and may aid by breaking the egg mass during hatching), high winds kill perch eggs in Oneida Lake through dispersal and physical destruction. Water currents generated by strong winds in 1974 displaced eggs from spawning sites to apparently less-hospitable areas in the lake while other eggs were

stranded on beaches (Clady and Hutchinson 1975). The major concentration of stranded eggs, although only a small fraction of those affected, was estimated by enumeration of subsamples to be almost 1% of the total egg potential (Clady and Hutchinson 1975). Damage to 16% of the perch eggs in an unfavorable year, resulting in the variation in observed total mortality between 82 and 98% (Table 2), might be attributed to direct effects of high winds. However, the consistent loss of over 80% of the young yellow perch in all years cannot be explained simply, although an even more extensive base mortality of over 99.9% also occurs for eggs and very young larvae of the walleye, another percid, in Oneida Lake (Forney 1976).

No evidence was found that would indicate that temperatures and wave action in Oneida Lake in 1969–75 were lethal to prolarval yellow perch. The progressive increase in density during the period of hatching (Fig. 1) suggests that mortality of pelagic prolarvae was low. In neither 1967 nor 1974 did the recruitment curve appear sharply dome shaped as would be anticipated if mortality were high. These curves are not conclusive evidence of low mortality of pelagic prolarvae, however, since recruitment to the pelagic stage (and sampling gear) is incomplete. Increase in population size could be partly due to hatching over a long period of time or increases in prolarvae vulnerability to the samplers. Nevertheless, increases in mean length and changes in length frequencies for 1974 (Fig. 2) indicate that many prolarvae that hatched early in the period survived to the larval stage. If recruitment of newly hatched larvae alone were expanding the population, distribution of lengths should remain relatively static.

Interactions between low temperature and high winds, and possibly other factors, result in the death of large numbers of yellow perch before cohorts become pelagic. Relatively low year-to-year variation in egg–prolarval mortality, especially from 1969 through 1972, suggests the existence of a complex of many interacting, relatively minor mortality factors rather than a single catastrophic event.

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Ecology of Euphausiids in the Gulf of St. Lawrence

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BERKES, F. 1976. Ecology of euphausiids in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 1894–1905.

Geographical and vertical distributions, reproduction, growth and maturity, food and feeding of *Meganyctiphanes norvegica*, *Thysanoessa raschii*, *T. inermis*, and *T. longicaudata* in the Gulf of St. Lawrence were studied, based on plankton samples from 10 cruises, largely from 2 consecutive yr. Adults of the first three species occurred most abundantly in the western Gulf and their larvae in the Magdalen Shallows. By contrast, *T. longicaudata*, an oceanic species, occurred mainly in the eastern Gulf year-round. All four species reached reproductive maturity at 1 yr of age; all but *T. longicaudata* populations contained at least two breeding year-classes. The three *Thysanoessa* species started spawning in April at the time of the phytoplankton bloom; *M. norvegica* was a summer breeder. All four species were omnivorous, but *M. norvegica* and *T. longicaudata* stomachs contained relatively more animal matter than those of the other two. These findings were supported by studies on the morphology of feeding appendages.

Thysanoessa longicaudata was differentiated from the other species mainly on the basis of distribution patterns, and *M. norvegica* from the remaining two mainly on the basis of differences in feeding and reproductive season. In contrast to relatively clear resource partitioning in five of the six species pairs, only relatively small differences in the stomach content composition in winter samples, the spacing of setules, and the length of the breeding season differentiated *T. inermis* from *T. raschii*.

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Des échantillons de plancton recueillis au cours de 10 croisières, en grande partie sur 2 a. consécutives, nous ont permis d'étudier la distribution géographique et verticale, la reproduction, la croissance et la maturité, et la nourriture et l'alimentation de *Meganyctiphanes norvegica*, *Thysanoessa raschii*, *T. inermis* et *T. longicaudata* dans le golfe Saint-Laurent. Les adultes des trois premières espèces se trouvent en plus grande abondance dans la partie occidentale du Golfe et leurs larves sur le plateau des îles de la Madeleine. Par contraste, *T. longicaudata*, une espèce océanique, se rencontre surtout dans la partie orientale du Golfe à l'année longue. Les quatre espèces atteignent la maturité sexuelle à l'âge de 1 a.; toutes les populations, sauf celles de *T. longicaudata*, contiennent au moins deux classes d'âge reproductrices. Les trois espèces de *Thysanoessa* commencent à pondre en avril au moment de la fleur de phytoplancton; *M. norvegica* pond en été. Les quatre espèces sont omnivores, mais les estomacs de *M. norvegica* et de *T. longicaudata* contiennent relativement plus de matière animale que ceux des deux autres espèces. Des études de la morphologie des appendices de nutrition corroborent ces observations.

Thysanoessa longicaudata se différencie des autres espèces principalement par sa distribution, et *M. norvegica* des deux autres espèces par des différences dans l'alimentation et la saison de ponte. La séparation de la ressource en cinq de six paires d'espèces est donc relativement claire. La paire *raschii–inermis* est toutefois difficile à séparer en dépit de différences possiblement significatives dans la durée de leur saison reproductive et dans le contenu stomacal d'échantillons d'hiver.

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EUPHAUSIID crustaceans are one of the commonest elements of marine zooplankton, but studies of their comparative ecology has been hampered by the lack of basic biological information. Some aspects of the biology of euphausiid species in the Chaleur Bay of the Gulf of St. Lawrence have been studied in detail (Lacroix 1961, 1968; Lacroix and Bourget 1973); however, the general biology of euphausiids in the Gulf has not been worked out to any extent (see Shih et al. 1971).

Detailed information is available on some species in some areas (Hollingshead and Corey

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1974), but none of the investigations on euphausiid communities directly addresses the question of niche differentiation. At least two studies on Atlantic Ocean species, however, offer considerable relevant material. Einarsson (1945) described the six resident North Atlantic species mainly with respect to their vertical and geographical distributions and found considerable overlap between several pairs of species. In a study of a much smaller area, the Clyde Sea in Scotland, Mauchline (1960, 1966) observed great overlap in the ecological requirements of the two species present, *Meganyctiphanes norvegica* and *Thysanoessa raschii*, but also some differences with regard to their stomach contents, feeding behavior, and vertical distributions.

The pelagic marine environment is relatively unstructured as compared to, for example, the benthic environment, and the apparent coexistence of planktonic populations has inspired much speculation with respect to the applicability of the principle of competitive exclusion (e.g. Hutchinson 1961).

There is a dearth of studies on resource partitioning among marine zooplankton. A detailed but incomplete review by Schoener (1974) cites only one marine planktonic example (Stone 1969), among 81 studies. Mullin (1967) has observed that there were probably no cases in which niche differentiation or resource partitioning has been worked out satisfactorily for marine copepods.

The Gulf, a semienclosed inland sea, is geographically well suited for such an investigation, containing a relatively small number of species compared to more southerly seas. The basic approach used in this study was to compile data on distributions, life cycles, and the food of the four species in the Gulf, *M. norvegica*, *T. raschii*, *T. inermis*, and *T. longicaudata*. These data were then synthesized into an assessment of the comparative ecology of the four species.

Materials and Methods

The study is based on quantitative plankton samples from nine cruises, nonquantitative samples from a 1967 cruise, a collection of April samples from the Strait of Belle Isle area, and samples from the Bonne Bay area, western Newfoundland. Dates of cruises, the number of stations, and the number of samples analysed are summarized in Table 1. Details of physicochemical measurements and other biological parameters at these stations are given in Bulleid and Steven (1972) and in Steven et al. (1973). Samples were preserved in 5% buffered Formalin in sea water. Analysis was usually done on a three-quarters subsample. All euphausiid identifications and terminology were based on Einarsson (1945).

About two thirds of all samples were taken with standard ¼-m white nylon nets of no. 6 mesh (aperture size about 0.24 mm). Most of the rest were taken with ½-m nets of no. 0 mesh (aperture size 0.57 mm). Nets were hauled at a speed of about 1 m/s and the towing time ranged from 5 to 30 min. All nets were metered, with one exception. The samples of the January cruise, in which only ¼-m no. 6 nets were used, were quantified as follows: the mean rate of water filtered per unit time in all metered no. 6 nets was multiplied by the length of tow of each of the samples of the January cruise.

Vertical distributions were determined from closed horizontal hauls, taken mostly in May and June. Most of the rest of the samples were taken in August, September, and November; April and July samples were underrepresented and there were no horizontal samples in January. Nets were fitted with messenger-operated opening–closing devices for all horizontal subsurface tows. The actual sampling depth in most cases was determined by the trace of a time–depth recorder attached to the hydrographic wire just below the net.

Life cycles of the four species were studied with respect to the onset and duration of their reproductive seasons, growth rates, age at reproductive maturity, and longevity. As there was no evidence to the contrary in the geographical distributions, each species was assumed to be represented by one and only one population in the Gulf. Growth and age were then determined by pooling all data for each cruise comprising of a set of stations and treating each cruise as a point in a time sequence.

Breeding seasons were determined by the presence or absence of spermatophores, the appearance of eggs and larvae in the plankton, and the relative size of the larvae at various points in time.

Food and feeding studies were based on an analysis of stomach contents and the functional morphology of the feeding appendages. Euphausiids dissected for stomach contents were adults and adolescents randomly chosen from May, August, and January samples. The occurrence of all identifiable items and the major constituent in each, as well as the degree of fullness of the stomach, were noted. Unidentifiable matter was classified as "mush."

Food overlap was calculated by the method given by Horn (1966):

$$\hat{C}\lambda = \frac{2\sum_{i=1}^{S} X_i Y_i}{\sum_{i=1}^{S} X_i^2 + \sum_{i=1}^{S} X_i^2}$$

where $\hat{C}\lambda$ = the overlap coefficient;
S = the total number of food categories;
X_i = that proportion of the total diet of species X taken from a given category of food i.

The overlap coefficient varies from 0 when the samples are completely distinct (containing no food

categories in common) to 1.00 when the samples are identical with respect to the proportions of food categories. A value $\geqslant 0.60$ is assumed to be a significant overlap (Zaret and Rand 1971).

Spacing of setae and setules on the Gulf euphausiids was measured on the ischium of the sixth thoracic appendages of adult female individuals; Nemoto (1967) has shown that the structure of the setae and the spacing between setules (also referred to in the literature as "bristles" or "barbs") are a good index of the relative importance of filter feeding in the nutrition of euphausiid species and of the particle sizes ingested.

Results

Distribution and Abundance

The earliest seasonal records of euphausiid larvae were from late April; however, there was no earlier sampling. Euphausiid spawning activity appeared to spread from east to west in the Gulf; first records were from the Cabot Strait area off Cape Breton and the Newfoundland coast, then in the southeast Magdalen Shallows, followed by the appearance of large numbers of larvae in the central and western Magdalen Shallows and the Gaspé area (Fig. 1). By the end of May, euphausiid larvae were found in all parts of the Gulf, except the estuary which was not sampled in spring.

In mid-May, highest numbers occurred in Magdalen Shallows and in the area between Bonne Bay and the north shore. In early June larvae were most abundant in the northern area and at the north-central edge of the Magdalen Shallows proper. At the peak of the spring spawning season, concentration of larval euphausiids ranged up to 800 individuals/m^3 over the whole water column. On the basis of oblique tows, the following average concentrations were obtained for the entire Gulf in the May 7–21 cruise: nauplius stage larvae, 20.7/m^3; calyptopis, 3.7/m^3; and furcilia, 0.1/m^3. The corresponding figures for the May 31–June 14 cruise were: nauplius, 2.6/m^3; calyptopis, 3.9/m^3; and furcilia, 1.9/m^3. Concentrations of larvae fell sharply after June, but small numbers were found sporadically in various parts of the Gulf through summer and fall.

Quantitative geographical distributions for each of the four species were determined on the basis of oblique tows only (see Table 1). Distribution and abundance of *M. norvegica* is given in Fig. 2A–D. Winter and spring samples indicated that the adults were present in the deeper parts of the Gulf, with the bulk of the population probably occurring in the western Gulf. August samples from 2 consecutive yr showed

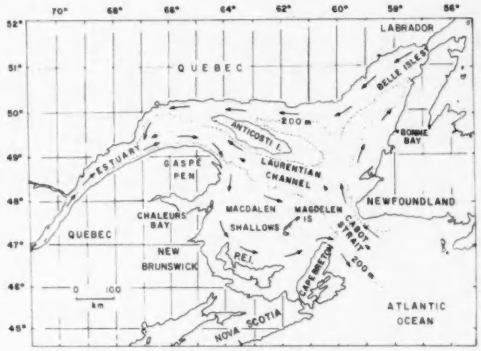

FIG. 1. The Gulf of St. Lawrence and the general pattern of currents. Dotted lines indicate deep currents. All currents are subject to annual, seasonal, and short-term variations in velocity. For more detail, see El-Sabh et al. (1969), Trites (1972), and El-Sabh (1976).

that the adult populations were again mainly concentrated in the west. Larvae, however, occurred largely in the Magdalen Shallows and the central Gulf in August. Samples in September and November showed larvae and adolescents in all parts of the Gulf. Results from successive cruises (not all shown in maps) were consistent with this general pattern.

Thysanoessa raschii distributions from a representative selection of six cruises are shown in Fig. 2E–G. In April and May, some adult *T. raschii* were found in all parts of the Gulf, and the bulk of the population occurred in the west. Summer samples showed a geographical separation of adults from larvae, most adults occurring in the western Gulf and most larvae in the Magdalen Shallows. By September, the populations of larvae and adolescents were dispersed in all parts of the Gulf, with the largest numbers in the Cabot Strait area, northern and eastern parts. Similarly, in November, adolescents were found dispersed in the Gulf, off the eastern tip of Anticosti Island and the Northwestern Newfoundland coast. In January, populations of adolescents were found in the western Gulf as well.

Only one distribution map of *T. inermis* is given (Fig. 2H). In April and May, adult *T. inermis* were most abundant in the western Gulf, northwest of Anticosti, and in the eastern Magdalen Shallows. The late spring distribution pattern was similar, with the exception that large numbers occurred immediately west of the Gaspé peninsula. Distribution of larvae was similar to that of *T. raschii*; the largest numbers occurred in the Magdalen Shallows. In contrast to *T. raschii*, however, *T. inermis* larvae were more

TABLE 1. Cruises and sampling data used for assessing the ecology of Gulf of St. Lawrence euphausiids.

	Date	No. of stn.	No. oblique tows	Total no. samples
CHS *Hudson*	Aug. 10–20, 1967	28	—	29
CSS *Dawson*	Jan. 9–22, 1969	18	23	23
MV *Ambrose Foote*	May 7–21, 1969	20	29	76
MV *Ambrose Foote*	May 31–June 14, 1969	24	41	132
MV *Ambrose Foote*	June 21–July 4, 1969	25	42	143
MV *Ambrose Foote*	July 30–Aug. 12, 1969	23	24	96
MV *Ambrose Foote*	Sept. 9–26, 1969	26	29	104
CNAV *Sackville*	Nov. 14–23, 1969	16	19	44
Arctic Biol. Stn. samples	Apr. 20–21, 1970	8	—	8
MV *Ambrose Foote*	Apr. 21–May 5, 1970	21	21	62
IBP — Bonne Bay samples	May–June 1970	1	20	20
MV *Ambrose Foote*	July 28–Aug. 27, 1970	29	29	67

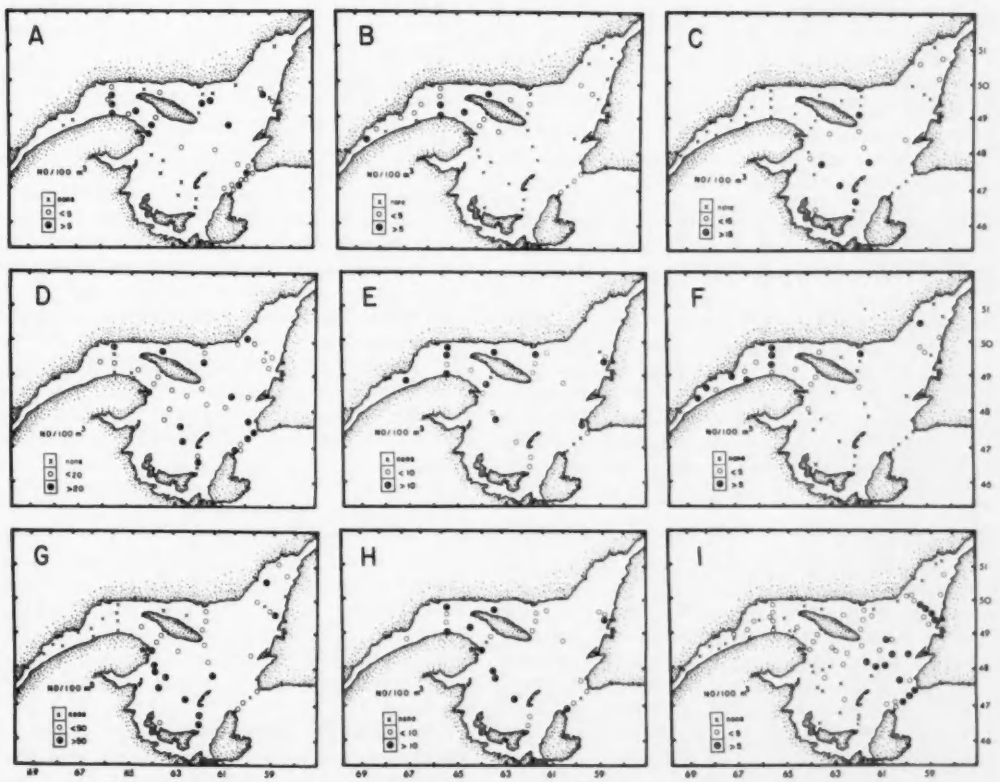

FIG. 2. Distribution and abundance of euphausiids in the Gulf of St. Lawrence. A, *Meganyctiphanes norvegica* adults in January 1969, May 1969, and April/May 1970; B, *M. norvegica* adults in August 1969 and August 1970; C, *M. norvegica* larvae in August 1969 and August 1970; D, *M. norvegica* larvae and adolescents in September 1969 and November 1969; E, *Thysanoessa raschii* adults in May 1969 and April/May 1970; F, *T. raschii* adults in August 1969 and August 1970; G, *T. raschii* larvae in August 1969 and August 1970; H, *T. inermis* adults in May 1969 and April/May 1970; I, *T. longicaudata* adults, all cruises.

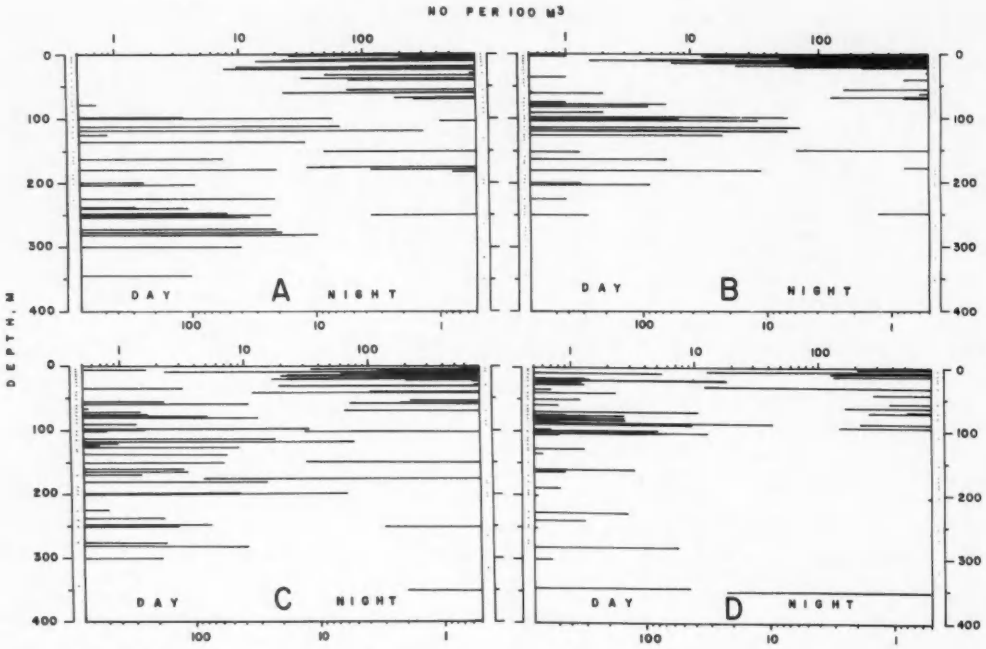

FIG. 3. Vertical distributions of adult euphausiids in the Gulf of St. Lawrence. A, *M. norvegica*; B, *T. raschii*; C, *T. inermis*; D, *T. longicaudata*. The upper x-axis belongs to the day data and the lower to the night data.

abundant in the eastern part of the Magdalen Shallows than in the western part. In September, larvae and adolescents were found in all parts of the Gulf but mostly in the east and the north. The general pattern in November followed that of September, with few young remaining in the Magdalen Shallows. In January, adolescents appeared to be evenly distributed in all parts of the Gulf.

Thysanoessa longicaudata was most abundant in the deep waters of the eastern Gulf in all seasons (Fig. 2I). Its distribution showed no discernible variation in time other than the early spring appearance of aggregations of sexually mature individuals in inshore areas off western Newfoundland. The seasonal pattern in abundance indicated a gradual depletion of adult animals through spring and summer, followed by an increase in numbers in fall and winter.

Day- and nighttime vertical distributions of the four species are given in Fig. 3. Each line represents one sample. Negative records are shown as dots on the margin; in the 0–100-m day samples, not all negative records are indicated due to lack of space. All data refer to adults and adolescents that have survived one winter.

Daytime populations of *M. norvegica* occurred near the seafloor in waters deeper than 100 m. The largest part of the population probably occurred below 200 m; however, the samples available for study probably underpresent the *M. norvegica* in the deeper waters of the Laurentian Channel.

At night, *M. norvegica* most commonly occurred between 10 and 30 m. Substantial numbers were found down to about 70 m, and a fraction of the population appeared not to take part in diurnal vertical migrations but to remain in the deeper waters. Most of the nighttime catches from near the surface were from the estuary where the thermocline remains relatively weak throughout the summer (Bulleid and Steven 1972).

Daytime depth distribution maximum of *T. raschii* occurred at about 100–200 m, with few deeper than 200 m. A daytime surface catch was obtained in November, and a 35-m daytime catch in the Magdalen Shallows, in spring. The nighttime catches were sharply concentrated in the upper 20 m, with part of the population occurring in the deeper waters.

Broad vertical distribution ranges characterized

T. inermis populations as compared to the other two in day and night samples. Most daytime samples came from 100 to 300 m, and night samples from 0 to 70 m.

Thysanoessa longicaudata, in contrast with the other species, occurred most commonly in the upper 100 m in the daytime samples. The depth range was large, however, and *T. longicaudata* was found even in the deepest horizontal samples available, 350 m. Nighttime vertical distribution was not clearly different from daytime distribution, but there was some evidence of an upward shift in the depth of population concentration.

In addition to these four species, all previously recorded from the Gulf (Shih et al. 1971), a total of five specimens of a fifth species, *Nematoscelis megalops* was recorded: two males (22 and 20 mm) and three immatures (18, 16, and 11 mm), all caught in deep hauls at Cabot Strait.

Life Cycles

Figure 4 shows the percentage of euphausiids carrying spermatophores. As euphausiid eggs are fertilized by spermatophores transferred from males to females, the presence of spermatophores in females is considered to be closely related to breeding activity (Drobysheva 1957; Mauchline and Fisher 1969).

All three *Thysanoessa* species appeared to be spring breeders, starting as early as mid- or late April. Spermatophore occurrence suggested a peak spawning period in April/May, which coincided with the spring phytoplankton bloom in the Gulf with the exception of the estuary area (Steven 1974).

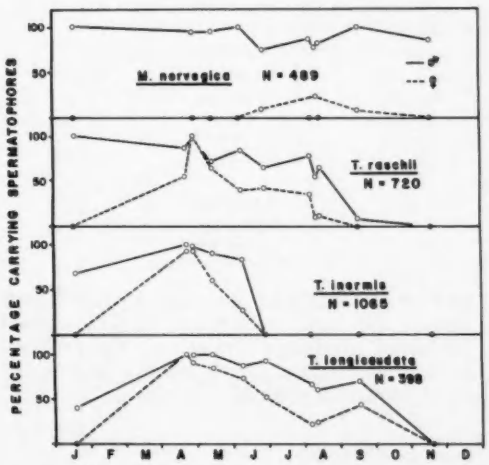
PERCENTAGE CARRYING SPERMATOPHORES
M. norvegica N = 489
T. raschii N = 720
T. inermis N = 1065
T. longicaudata N = 398
100
50
J F M A M J J A S O N D

FIG. 4. Seasonal variation in the percentage of euphausiids carrying spermatophores. Each symbol represents one cruise, taking the midpoint of each cruise (see Table 1).

Thysanoessa inermis that appeared to start spawning shortly before *T. raschii* in spring had a relatively shorter reproductive season that ended before the end of June. *Thysanoessa inermis* occurring sympatrically with *T. raschii* in the estuary area in summer and fall were not in breeding condition.

The youngest larvae were not separated by species for the lack of reliable, objective, taxonomic criteria. However, judging from the sexual maturity of the adults and from the percentages of males and females carrying spermatophores, the earliest larvae in spring were probably those of *T. inermis*. This is reflected in the relative size of larvae of *T. inermis* and *T. raschii* in the August samples (Fig. 5).

In contrast to the *Thysanoessa* species, there was no evidence in 2 yr data that M. norvegica spawned at all in spring. The earliest field evidence of *M. norvegica* spawning activity was on July 1, 1969, off Gaspé. Most spermatophore-bearing females were obtained from stations at which large numbers of euphausiid eggs also occurred. Percentage of *M. norvegica* females with spermatophores was small at all times, as noted earlier by other investigators (Einarsson 1945). Spermatophores tore away easily from preserved female *M. norvegica*; they were relatively more firmly attached in *Thysanoessa*.

Size at maturity may be defined as the smallest size at which 50% of the individuals were carrying developed spermatophores in the breeding season. Thus, size at maturity of the four species were 22, 16, 18, and 10 mm for *M. norvegica*, *T. raschii*, *T. inermis*, and *T. longicaudata*, respectively. All four species were breeding at 1 yr of age; those individuals of the year-class that were immature at the beginning of the breeding season were all, or almost all, mature by the end of the breeding season. This may be seen by comparing size at maturity with growth rates given in Fig. 5 which summarizes length-frequency relationships.

As euphausiids molt periodically, growth rates and age may be determined only by inference from length-frequency histograms. *T. longicaudata* populations were unimodal, but the other three species showed bimodal size-frequency distributions. Tracing the life cycle of *T. raschii* from Fig. 5, we see that the 0 age-group (0-gr), which was spawned largely in April/May, appeared as 5–8-mm larvae in August, recorded in 1969 and 1970. (The larvae were not sorted out in the 1967 samples.) The 0-gr *T. raschii* became

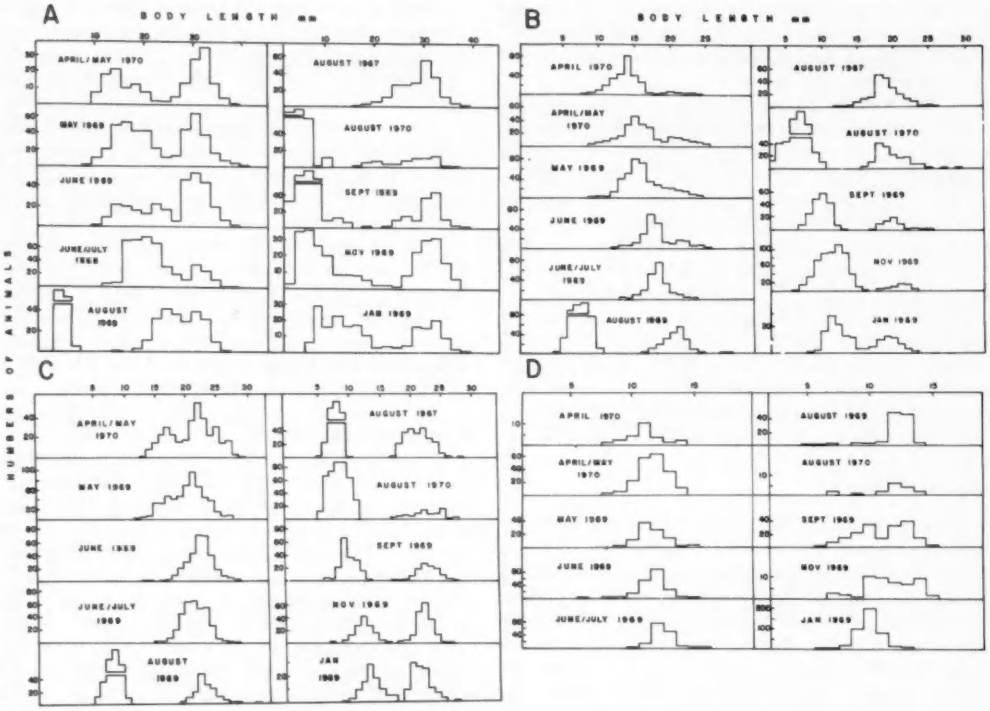

FIG. 5. Length-frequency distribution of euphausiids in the Gulf of St. Lawrence. A, *M. norvegica*; B, *T. raschii*; C, *T. inermis*; D, *T. longicaudata*.

TABLE 2. Maturity and breeding of euphausiids in the Gulf of St. Lawrence. Reproduction begins at age 1 for all four species.

Species	Size at maturity (*mm*)	No. years breeding	Breeding season
M. norvegica	22 (male only)	2+	July–Oct.
T. raschii	16	2+	Apr.–Sept.
T. inermis	18	2+	Apr.–June
T. longicaudata	10	1+ (?)	Apr.–Oct.

the 1-gr after spawning the following spring, continued to grow, and merged with the slower-growing older age-class(es) after June. In contrast to *M. norvegica* and *T. inermis*, the older size-groups of *T. raschii* seemed to be largely replaced every year.

The large segment of the *M. norvegica* and *T. inermis* populations are represented by the older size-group of the bimodal distribution. This may be explained by year-class strength phenomena, or perhaps more likely, by the accumulation of slow-growing older age-classes. In any case, the maximum longevity cannot be determined, but it may be deduced that the populations of both species, and those of *T. raschii* as well, contain individuals of at least 2 yr of age. Table 2 summarizes information on the maturity and breeding of euphasiids in the Gulf.

FOOD AND FEEDING

The frequency of occurrence of various items in the stomachs of euphausiids is given in Table 3, and the frequency of occurrence of an item as the major constituent among stomach contents, in Table 4. Stomach contents of all four species

TABLE 3. Frequency of occurrence (by percentage) of various items in the stomachs of Gulf of St. Lawrence euphausiids.

	No. in sample	"Mush"	Dinoflagellates	Crustacean remains	Mud	Diatoms	Eggs	Euphausiid eyes	Tintinnids	Chaetognaths	Radiolarians	Foraminifers
January												
M. norvegica	43	56	14	88	12	—	—	—	2	2	—	—
T. raschii	26	38	4	8	69	—	—	—	—	—	—	—
T. inermis	52	31	4	12	10	2	—	—	—	—	—	—
T. inermis f. *neglecta*	38	32	5	26	—	8	—	—	—	—	—	—
T. longicaudata	51	67	12	63	—	12	12	—	8	—	—	—
August												
M. norvegica	72	86	42	94	—	—	—	4	—	1	1	1
T. raschii	37	81	51	32	—	—	—	3	3	—	—	—
T. inermis	50	92	76	38	—	—	—	—	—	—	—	—
T. inermis f. *neglecta*	36	58	6	64	—	6	—	—	—	—	—	—
T. longicaudata	20	45	50	45	—	15	—	—	20	—	—	—
May												
M. norvegica	30	67	10	87	—	37	—	—	13	—	—	—
T. raschii	37	84	3	11	—	46	38	—	22	—	—	—
T. inermis	38	68	11	29	—	32	18	—	29	—	8	3
T. inermis f. *neglecta*	41	68	—	34	—	22	—	—	12	—	—	—
T. longicaudata	29	38	3	55	—	7	21	—	10	—	—	—
Total	600											

TABLE 4. Major food item (by percentage) in the stomachs of Gulf of St. Lawrence euphausiids.

	No. in sample	"Mush"	Dinoflagellates	Crustacean remains	Mud	Diatoms	Eggs	Euphausiid eyes	Tintinnids	Stomachs > half full	Stomachs < half full	Stomachs empty
January												
M. norvegica	43	28	—	63	7	—	—	—	—	84	14	2
T. raschii	26	8	—	—	65	—	—	—	—	54	19	27
T. inermis	52	21	—	7	10	—	—	—	—	19	19	62
T. inermis f. *neglecta*	38	13	—	21	—	—	—	—	—	18	16	66
T. longicaudata	51	35	2	24	—	8	—	—	—	39	30	31
August												
M. norvegica	72	47	—	50	—	—	—	—	—	61	36	3
T. raschii	37	68	3	13	—	—	—	3	—	60	27	13
T. inermis	50	86	2	4	—	—	—	—	—	52	40	8
T. inermis f. *neglecta*	36	44	—	33	—	—	—	—	—	36	42	22
T. longicaudata	20	30	25	20	—	5	—	—	—	60	20	20
May												
M. norvegica	30	30	—	56	—	7	—	—	—	73	20	7
T. raschii	37	68	—	—	—	8	8	—	—	19	65	16
T. inermis	38	61	—	8	—	2.5	—	—	2.5	26	48	26
T. inermis f. *neglecta*	41	61	—	12	—	—	—	—	—	27	46	27
T. longicaudata	29	17	—	48	—	—	7	—	—	34	38	28
Total	600											

suggest omnivorous feeding, with animal and plant materials as well as unidentifiable matter, perhaps largely detritus, in the gut.

In *M. norvegica* stomachs, crustacean remains were the major constituent, followed by unidentifiable matter and plant material, in that order. Diatoms were common in the stomachs in May, dinoflagellates in August, and mud in January; mud was distinct from "mush" in being opaque and consisting of clay or silt-sized mineral grains.

Thysanoessa raschii stomachs contained "mush" as the predominant item in May and August samples and mud in January. Crustacean fragments occurred as a major ingredient only in August. May samples contained many diatoms and invertebrate eggs.

In *T. inermis* stomachs, "mush" was the most abundant item, followed by mud and crustaceans in January, dinoflagellates and crustaceans in August, and crustaceans, diatoms, and tintinnids in May. *T. inermis* in the tables refers to the *inermis* form of the species with the thoracic legs of uniform length. *Thysanoessa inermis* f. *neglecta* which has elongated second thoracic legs and constitutes about 7% of the population larger than 18-mm length (Berkes 1976), appears to differ from *T. inermis* in having a greater amount of crustacean material and a lower diversity of items in the stomach.

Thysanoessa longicaudata stomach contents from August and January showed a predominance of unidentifiable matter over animal food remains; this situation was reversed in May. Dinoflagellates and diatoms appeared as major items in both January and August, and invertebrate eggs in May.

The overlap coefficients were calculated from the data in Table 4, adjusted to eliminate "empty" as a category. *Thysanoessa inermis* refers to *inermis* form animals only. *Thysanoessa inermis* f. *neglecta* was left out of the calculation because it represents a small percentage of the total *T. inermis* population.

Results (Table 5) indicate significant overlaps in all possible combinations of the four species in August. In January, there were significant overlaps among all possible combinations of three of the four species, excluding *T. raschii*. May samples indicated significant overlaps between *M. norvegica* and *T. longicaudata* and between *T. raschii* and *T. inermis* only.

The spacing of the filtering structures on thoracic appendages showed that the distances between adjacent setules were about 25 μm in *M. norvegica*, 6–8.5 μm in *T. raschii*, 8–9 μm in *T. inermis*, and 14–20 μm in *T. longicaudata*. These values are thought to correspond to the smallest particle size that can be efficiently retained by the filter of the thoracic legs (see Parsons et al. 1967). The setae are reinforced with spines in *M. norvegica* and *T. inermis*, but not in *T. raschii*. In all three species, the setae are long and distance between adjacent setae are small so that the setae make up a closed lattice. *Thysanoessa longicaudata*, by contrast, has proportionately shorter setae than the others, and the setae do not form a closed filtering lattice.

TABLE 5. Food overlap coefficients (Horn 1966) of the four species of euphausiids in the Gulf, based on stomach content samples taken in January, May, and August. Index varies from 0, when the contents are entirely distinct, to 1.00 when they are identical.

	T. raschii	*T. inermis*	*T. longicaudata*
January			
M. norvegica	0.14	0.68	0.82
T. raschii	—	0.47	0.09
T. inermis	—	—	0.88
May			
M. norvegica	0.46	0.57	0.98
T. raschii	—	0.98	0.34
T. inermis	—	—	0.45
August			
M. norvegica	0.82	0.69	0.78
T. raschii	—	0.97	0.73
T. inermis	—	—	0.63

Ecological differences among the four species with respect to their geographical distributions, day and night vertical distributions, stomach contents in January, May, and August, spacing of setules, and onset and duration of breeding seasons are summarized in Table 6.

Discussion

Geographical distributions of the four species in the Gulf indicate two basic patterns: three of the species, *M. norvegica*, *T. raschii*, and *T. inermis* show a pattern in which most of the adult population is concentrated in the western Gulf during the breeding season (see also Sameoto 1976). Larvae of these species are found mainly in the Magdalen Shallows area, downcurrent from the western Gulf. Larvae in the Magdalen Shallows are presumably retained there perhaps for several months by the slow circulation pattern. Population concentrations gradually disperse out of the Magdalen Shallows in late larval or early adolescent life, by which time extensive diurnal vertical migrations have started (Lacroix 1961). Once outside the Shallows and in the deeper waters of the Laurentian Channel, deep-

TABLE 6. Ecological differences among the four species of euphausiids in the Gulf of St. Lawrence. "S" denotes an an apparent significant difference.

Special pairs	Geogr. distrib.	Vert. distrib.		Stomach contents			Spacing of setules	Breeding season	
		Day	Night	Jan.	May	Aug.		Onset	Duration
M. norvegica–									
T. raschii	—	S	—	S	S	—	S	S	—
M. norvegica–									
T. inermis	—	—	—	—	S	—	S	S	S
M. norvegica–									
T. longicaudata	S	S	S	—	—	—	—	S	—
T. raschii–									
T. inermis	—	—	—	S	—	—	—	—	S
T. raschii–									
T. longicaudata	S	—	S	S	S	—	S	—	—
T. inermis–									
T. longicaudata	S	—	S	—	S	—	S	—	S

migrating euphausiids would come under the influence of westerly flowing deep currents. The distribution maps show that over a period of several months (August to the following winter and spring) the proportion of the euphausiid population occurring in the western Gulf gradually increases. By the following reproductive season, the bulk of the adult population, 1 yr old and older, is concentrated in the main breeding area of the three species.

This seasonal distribution pattern suggests adaptations not only for the maintenance of the populations in the Gulf, but also for an efficient use of food resources. The main spawning area of the three species coincides with the zone of the highest primary production in the Gulf (Steven 1974).

Distribution of *T. longicaudata* shows a different pattern: the main concentration of the species occurs in the eastern Gulf, year-round. This result is consistent with the hypothesis that there are two large gyres, one in the eastern Gulf and one in the west, divided at about the 100-m level south of Anticosti (El-Sabh 1976). A biological consequence of this partial separation of the eastern basin, if real, would be that populations confined mainly to the upper 100 m would tend to be retained there, whereas populations with a deeper vertical distribution would be carried with the deep flow to the western Gulf.

Thysanoessa longicaudata is in fact found mainly in the upper 100 m day and night, whereas the other three species occur deeper than 100 m during the day. This biological verification of El-Sabh's (1976) geostrophic flow calculations remains speculative, however, for the lack of year-round direct current measurement data.

The ecological significance of this distribution pattern as opposed to its mechanism (Dunbar 1968) may be related to the biological requirements of *T. longicaudata*, known to be a pelagic species in other parts of its range (Einarsson 1945). It has coarse, short setae unlike those of filter-feeding euphausiids, and elongated second thoracic legs and bilobed eyes suggesting adaptations for feeding on large particles. *Thysanoessa longicaudata* thus appears to be well adapted for life in a nutritionally dilute environment such as the eastern Gulf (Steven 1974). Furthermore, only the eastern Gulf supports large populations of other oceanic zooplankton such as the carnivorous hyperiid amphipods *Parathemisto abyssorum* and *P. gaudichaudi* which have distribution patterns similar to that of *T. longicaudata* (Hoffer 1971).

Data on food and feeding distinguish *M. norvegica* from *T. raschii* and *T. inermis*. In all seasons, crustacean remains were the most important item in *M. norvegica* stomachs, whereas the *Thysanoessa* contained mainly detritus-like material and relatively little identifiable animal food. A study of the feeding appendages indicate that there may be further differences in the size of particles ingested. *Meganyctiphanes norvegica*, with a minimum spacing of about 25 μm between setules on the setae of thoracic appendages, is probably unable to utilize food particles at the lower end of the size range of particles available to *T. raschii* (6 μm) and *T. inermis* (8 μm). In view of this, the fairly high food overlap coefficient values between *M. norvegica* and *T. inermis*, as determined from gross stomach content analyses, 0.57, 0.68, and 0.69 for the three periods of sampling (Table 5) are probably overestimates. In reality, the food divergence

between the two is likely to be greater, and greater still between *M. norvegica* and *T. raschii*.

Unrecognizable stomach contents, "mush," may have consisted of detritus, naked flagellates, half-digested soft parts of plankton, or any combination of these. Some of the "mush" appeared as 10–18 μm unornamented oval outlines under the microscope but could not be readily attributed to phytoplankton material (see Mauchline 1960).

The ratio of the minimum spacing in *T. inermis* adults (8 μm) to that in *T. raschii* (6 μm), yields 1.3 resembling the Hutchinsonian index of 1.2–1.4 which has been empirically found to be a common ratio of the feeding parts of otherwise similar species in many groups (Schoener 1974). This difference may permit niche diversification by size-selective feeding by the two species, a hypothesis testable in the laboratory. Even allowing for such differences, the food overlap coefficient between the two species, 0.98 in May and 0.97 in August, indicated a high degree of similarity. In January, however, the coefficient was only 0.47, reflecting food divergence attributable to the importance of bottom mud in *T. raschii* stomachs but not in *T. inermis*. This finding may be significant on two counts. First, seasonal differences, often poorly investigated in plankton work, may be the key to food diversification. Secondly, as Zaret and Rand (1971) have argued, a reduced food overlap between two species in the season of lowest food abundance may provide evidence of competition.

Life-history characteristics further differentiate *M. norvegica*, breeding from July to October, from the *Thysanoessa* species having peak reproductive activity in late April and May, corresponding to the spring phytoplankton bloom in the Gulf (Steven 1974). The staggering of breeding activity may act to decrease possible competitive interactions between larvae of *M. norvegica* and those of *Thysanoessa*.

The difference in the onset of breeding activity between *T. raschii* and *T. inermis* is within the range of sampling error and year-to-year variations, but the duration of the breeding season is unmistakably different over 2 yr. The extended reproductive season of the *T. raschii* population may be an adaptive mechanism by which the population may still reproduce itself in years of poor spring breeding success. Following such a year or series of years, *T. raschii* may be relatively more abundant than *T. inermis*, whereas years leading to successful spring euphausiid breeding may favor a relatively higher ratio of *T. inermis* to *T. raschii*. This is a testable hypothesis that requires several years' data on relative abundances. Lacroix's (1968) study in Chaleur Bay and Drobysheva's (1957) in the Barents Sea have indicated such fluctuations in the ratio of *T. raschii* to *T. inermis*. Some investigators have argued that the alternating dominance of ecologically similar zooplankton species indicates competition (Pejler 1962).

Ecological differences among the four euphausiid species in the Gulf, as summarized in Table 6, show that the niches of all but one of the species pairs may be separated relatively unambiguously. But differences between *T. raschii* and *T. inermis* seem relatively slight, as previously pointed out by Dunbar (1968). The existence of some differences may be demonstrated; the analysis also indicates, however, two lines of indirect evidence for competition.

Variability within the *T. inermis* population may provide an adaptive response for the reduction of competitive interactions. The *neglecta* form of *T. inermis* appears to be morphologically better adapted than the typical *inermis* form for feeding on large particles and tends to have more animal food in the stomach contents (Tables 3 and 4). The presence of the *neglecta* morph may increase the range of resources available to the *T. inermis* population as a whole, since the two forms come from the same adult stock (Berkes 1977).

It is difficult, if not impossible at present, to establish the degree of niche diversification that is necessary to permit coexistence. But apparently there are a constellation of factors that may assure the coexistence of zooplanktonic species even as closely related and ecologically similar as *T. raschii* and *T. inermis*.

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Selection of Artificial Spawning Sites by the Spotfin Shiner (*Notropis spilopterus*)

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GALE, W. F., AND C. A. GALE. 1976. Selection of artificial spawning sites by the spotfin shiner (*Notropis spilopterus*). J. Fish. Res. Board Can. 33: 1906–1913.

In 1975 experiments were conducted in the Susquehanna River, near Berwick, Pennsylvania, to investigate spawning-site selection of the spotfin shiner (*Notropis spilopterus*), a crevice spawner. Results of experiment A revealed that visual cues and water currents were important in spawning-site selection. Spotfins deposited 43,638 eggs on black discs and only 2 eggs on clear discs; 87% of the eggs were in horizontal crevices and the remainder in vertical crevices paralleling (7%) and perpendicular (6%) to the current. Fish spawned over the entire disc in slow currents but avoided strong currents (0.57 m/s) by spawning on the downstream side of the discs. Nearly 90% of the eggs were deposited in crevices 1.5 and 3.0 mm wide, the two smallest sizes. In angular crevices 15–90° from horizontal, fish deposited 74% of 8,358 eggs in the 15° crevice and 24% in the 30° crevice.

In experiment B, a stack of black acrylic plates was placed near the river surface, at midwater, and near the bottom; in July fish deposited 91% of 13,088 eggs in the bottom stack. By mid-August stack usage had changed and 80% of 11,456 eggs were in the surface stack; the others were in the midwater stack. Rate of egg deposition on acrylic plates between July 10 and August 20 peaked in early August.

In experiment C, 95% of 46,328 eggs were placed in crevices between blue (55%) and black (40%) plates; other colors were green (4%), red (1%), and white, yellow, and orange (< 1%). Fish usually spawned on the plates between 0600 and 1000; spawning did not occur at night.

The spotfin has potential as a bioassay organism because of its wide distribution, the ease with which large numbers of its eggs can be collected, its extended breeding season, and the simplicity of rearing the young.

GALE, W. F., AND C. A. GALE. 1976. Selection of artificial spawning sites by the spotfin shiner (*Notropis spilopterus*). J. Fish. Res. Board Can. 33: 1906–1913.

Nous avons poursuivi des expériences en 1975 dans la rivière Susquehanna, près de Berwick, en Pennsylvanie, sur le choix des frayères par le méné bleu (*Notropis spilopterus*), un poisson qui fraie dans les crevasses. D'après les résultats de l'expérience A, les indices visuels et les courants jouent un rôle important dans le choix des frayères. Les ménés bleus déposent 43 638 œufs sur des disques noirs et seulement 2 œufs sur des disques clairs; 87% des œufs se trouvent dans des crevasses horizontales, la balance dans des crevasses verticales parallèles (7%) et perpendiculaires (6%) au courant. Les poissons frayent sur toute la surface du disque dans des courants lents, mais évitent de forts courants (0.57 m/s) en frayant sur le côté d'aval des disques. Près de 90% des œufs sont déposés dans des crevasses de 1.5 et de 3.0 mm de largeur, les deux plus petites crevasses. Dans des crevasses faisant avec l'horizontale un angle de 15–90°, les poissons déposent 74% de 8 358 œufs dans la crevasse à 15° et 24% dans la crevasse à 30°.

Dans l'expérience B, des plaques acryliques noires furent placées en piles près de la surface, à mi-profondeur et près du fond de la rivière; en juillet, les poissons déposent 91% de 13088 œufs dans la pile du fond. A la mi-août, l'usage des piles change et 80% de 11 456 œufs sont déposés dans la pile de surface; les autres, dans la pile du milieu. Le rythme de déposition des œufs sur les plaques acryliques entre le 10 juillet et le 20 août atteint un sommet au début d'août.

Dans l'expérience C, 95% de 46 328 œufs sont placés dans des crevasses entre des plaques bleues (55%) et noires (40%); les autres couleurs sont le vert (4%), le rouge (1%) et le blanc, le jaune et l'orange (<1%). Les poissons frayent sur les plaques ordinairement entre 0600 et 1000; ils ne frayent pas la nuit.

Le méné bleu pourrait être utilisé dans des essais biologiques: il a une répartition étendue, ses œufs peuvent être recueillis facilement en grand nombre, sa saison de ponte est longue et l'élevage des jeunes est simple.

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DURING the summer of 1974 thousands of fish eggs were found within the crevices of a multiple-plate sampler (for benthic sampling) in the Susquehanna River's north branch near Berwick, Pennsylvania. Some of the eggs were hatched and the larvae reared to a size sufficient to be identified as spotfin shiners (*Notropis spilopterus*). Large multiple-plate samplers (black acrylic) were spawned upon more often than small samplers (brown masonite) and small crevices seemed to be preferred to large ones. Our basic objective in 1975 was to investigate spawning-site preferences. Because of high turbidities stemming from acid mine drainage, direct observation of spotfin in the river near Berwick was impossible; therefore, spawning behavior was investigated indirectly by using acrylic plates (square) and discs as artificial spawning sites. Some observations of spawning spotfins were made downriver at Port Trevorton, Pennsylvania, where the water was clear.

Materials and Methods

EXPERIMENT A

Three stacks of nine black and one stack of nine clear acrylic discs (0.6 × 20 cm) with 1.5–12.0-mm spaces (1.5-mm increments) between them were placed in a holder about 25 cm above the river substrate to determine the position and sizes of crevices preferred by spotfins for spawning and to evaluate effects of current on egg deposition. Three zones and 12 sectors were etched on the disc surfaces (Fig. 1A) so that egg location could be recorded precisely. One black and one clear stack of discs were placed vertically in the water column; two stacks were placed horizontally, one headed into the current, and the other crosscurrent (Fig. 1B). The discs remained in the river until fish spawned on them (1 or 2 days) and then were taken to the laboratory so eggs could be scraped off with a rubber spatula and counted; some eggs from this and other experiments were hatched and the larvae reared in the laboratory for identification.

Of the five trials conducted, two were in slow-moving water (velocity near the bottom 0.23 m/s) about 1 m deep, 20 m from shore; one was near the channel in moderately fast water (velocity 0.45 m/s) about 2 m deep, and two were in fast water (velocity 0.57 m/s) about 1 m deep, just below a riffle. Position of discs within a stack and placement of the stacks on the holder were varied.

Crevice selection was investigated also with a black acrylic plate containing strips across it at angles of 15, 30, 45, 60, 75 and 90° from horizontal (Fig. 1C); the plate was mounted on a metal holder about 10 cm above the river bottom. The plate was placed in the channel or in a riffle for 24-h periods; on all but a few occasions, when the plate was turned cross current, the crevices opened downstream.

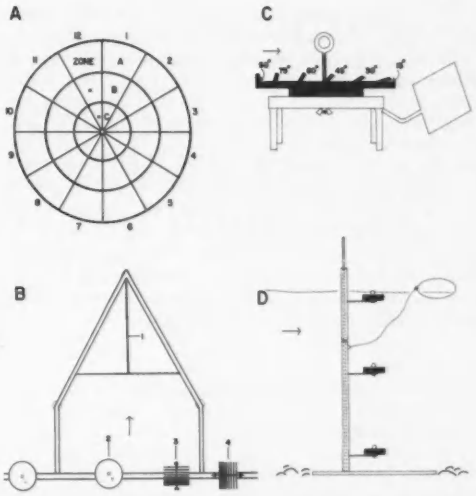

FIG. 1. Artificial spawning structures used in an investigation of factors involved in spawning site selection by the spotfin shiner (*Notropis spilopterus*). Arrows denote current direction. A, Upper surface of acrylic disc showing 3 zones and 12 sectors; B, Stacks of acrylic plates on their holder (top view): 1) fin, 2) vertical plates, 3) horizontal plates parallel to current, 4) horizontal plates cross current; C, Angular crevice device (side view); D, Device used to determine spawning depth preferences.

EXPERIMENT B

To determine if spotfins preferred a particular depth for spawning, three vertical stacks of five black acrylic plates (0.6 × 20 × 20 cm), separated by 3.0-mm spaces, were fastened to metal pipes which slipped over a vertical steel rod in the channel (Fig. 1D). Short sections of pipe were used for easy handling; the lower section was retrieved with a string and buoy. A stack of plates was placed about 10 cm from the river bottom, about 10 cm from the river surface, and midway to the bottom; stacks removed for egg counts were replaced by clean ones. In August, because of the large numbers of eggs (over 20,000) on some stacks, numbers of eggs were estimated by dividing total egg weight (oven dried at 105 C for 24 h) by a mean egg weight of 0.157 mg (based on weight of 34,000 eggs from four samples) instead of by direct enumeration.

To discover if spotfins spawned in shallow water nearshore, additional stacks of black acrylic plates were placed within 20 cm of the riverbank in water 15–20 cm deep. To determine if spotfins would spawn in shallow water near vegetation, plates were placed in water 15–30 cm deep at the edge of a bed of water willows (*Justicia americana*) growing on an intermittent island adjacent to the channel.

EXPERIMENT C

To determine if spotfins preferred certain colors of substrate for spawning, a vertical stack of 14 (0.6

× 20 × 20 cm) colored acrylic plates was placed on a steel holder 10 cm above the river (channel) bottom. Pairs of black, blue, green, orange, red, white, and yellow plates were in each stack; plates of similar color were separated by 3.0-mm spaces. Color arrangement was randomly determined for each pair of colors for each stack. From July 11 through July 31, plates were examined at 2-h intervals from 0600 to 2200 to determine spawning time. From August 1 through August 20, colored plates were checked daily at about 1600. Stacks removed for egg counts were immediately replaced by another. To supplement the data collected in the channel, an additional one or two stacks of colored plates were sometimes placed below a riffle, about 200 m farther upriver.

Results and Discussion

Aspects of Reproduction

Some general aspects of spotfin reproduction should be considered before discussing the results of various experiments.

Eggs and fry — A total of 100 eggs (preserved in 10% Formalin) from three different collections of spotfin eggs averaged 1.41 ± 0.08 mm in diameter. Measurements were made using an ocular micrometer. Live spotfin eggs measured by Stone (1940) averaged 1.5 mm; those preserved in Formalin were 1.4 mm in diameter. Spotfin eggs are pale yellow and adhesive when spawned; in our study, eggs at about 22 C began hatching in 6 days. Fry preserved in 10% Formalin had a mean total length of 4.79 ± 0.14 mm. Newly hatched fry remained quiescent on the bottom of hatching tanks for a few days before their mouths opened; food could not be observed in them until they were 7 days old. Spotfin fry were fed a finely textured commercial fish food (Tetramin E).

Spawning duration — In 1974 eggs were first found in the river on June 10 when the river temperature was 22.7 C and the last ones were collected on August 27 (river temperature 23.1 C). In 1975 we did not search for eggs until larvae became abundant in net samples and the first eggs were not collected until July; the last eggs were found on August 20. Individual females we examined contained eggs in several different stages of development. On this basis we assume the spotfin to be an intermittent spawner. Stone (1940) concluded that some spotfins in New York spawned at least twice in the same year. Nikolsky (1963) points out that "fractional" or intermittent spawners are less likely to lose an entire generation due to unfavorable environmental conditions. Also, fractional spawning would enable spotfins to utilize a spawning crevice more than once; this would be an important advantage if spawning crevices were in short supply, and there is some evidence that they were.

Spotfins examined by Stone (1940) contained from 225 to 1,580 ripe or nearly ripe eggs. Large fish contained more eggs than did small fish and females began spawning in their second or third summer. Fflieger (1965) observed that only a few of the spawning spotfins he examined were in their second summer; most were in their third.

Spawning behavior — At Port Trevorton, male spotfins established small breeding territories that included at least one crevice in the rocky substrate. Territories were defended with threat displays and physical attacks. Males usually spawned with one female at a time but spawned repeatedly with various members of a group of females that waited near the spawning crevice. Spotfin spawning in aquaria and on logs in Ohio streams is described by Pflieger (1965). Hankinson (1930) and Trautman (1957) provide brief descriptions of spotfins spawning under or on the bark of submerged logs and limbs.

Egg deposition — That over 99% of the eggs found were within crevices is probably a result of two factors. First, eggs may be directed with considerable accuracy because the spotfin has a "urogenital papilla" (Fflieger 1965) resembling the "ovipositor" of the fathead minnow (*Pimephales promelas*) pictured by Flickinger (1969). Raney (1940) described a similar structure, the "anal papilla," on blacknose dace (*Rhinichthys atratulus*). Second, underwater observations at Port Trevorton revealed that spawning spotfins of both sexes eat eggs that are left exposed on the substrate. Pflieger (1965) observed that males in aquaria ate eggs that missed the spawning site. Over 100 eggs were found in the stomachs of some males that had been spawning in a stream.

Spawning habitat — Spotfin eggs were found in stacks of acrylic plates, at least once, in nearly every habitat we could discern in the river. Spawning occurred near shore in water 15 cm deep and in the channel in water over 2 m deep. Eggs were found near the river surface and bottom, in quiet water along the shore, and in turbulent riffles near the middle. Spawning occurred near the plant beds and in open water far from vegetation. Pflieger (1965) observed that spotfins spawned among tree roots and under or within furrows in the bark of submerged logs. Spawning sites were "usually located near riffles, and invariably there was at least a slight current."

The large number of eggs deposited on the

TABLE 1. Effects of alignment with stream flow of artificial spawning structures (stacks of black acrylic discs) on their utilization by the spotfin shiner (*Notropis spilopterus*). Mean number and percent total spotfin eggs in Zones A, B, and C are adjusted to equalize surface area; overall percent total is unadjusted.

Trials	Current (*m/s*)	Zone	Stack position: Vertical	Horizontal (crosscurrent)	Horizontal (into current)	% Total
2	0.57	A	2,738	593	0	79.6
		B	465	177	0	15.4
		C	53	161	0	5.1
		% Total	(77.8)	(22.2)	(0)	
1	0.45	A	8,655	213	222	58.2
		B	4,141	34	139	27.6
		C	1,899	16	293	14.1
		% Total	(94.1)	(1.7)	(4.2)	
2	0.23	A	6,552	304	448	43.1
		B	8,862	383	946	48.7
		C	789	495	435	8.2
		% Total	(84.3)	(6.2)	(9.5)	
		Overall % Total (unadjusted)	(86.6)	(7.3)	(6.1)	

TABLE 2. Relationship between width of crevices and number of eggs of the spotfin shiner occurring in them. Crevices were formed by stacks of black acrylic discs.

Crevice width (*mm*)	1.5	3.0	4.5	6.0	7.5	9.0	10.5	12.0
No. of eggs	16,128	23,070	2,732	891	761	45	8	3

black acrylic discs in experiment A (Table 1) indicates that spotfins found the apparatus a highly desirable spawning site. In an attempt to simplify egg enumeration, discs in trials 4 and 5 (fast water) were removed after 1 day instead of the usual 2; even so, a surprisingly large number of eggs were collected. This experiment answered several basic questions: spotfins preferred small (1.5 and 3.0 mm) horizontal crevices, and some eggs traveled 10 cm or more toward the center of the discs before adhering; visual cues and water currents were important in spawning-site selection.

Nearly 90% of the more than 43,000 eggs collected in experiment A were in the 1.5- and 3.0-mm crevices (Table 2), and clearly these sizes were much preferred. Although the 3.0-mm crevice contained the most eggs, egg density (eggs per unit of space) was maximum in the 1.5-mm crevice and the latter was probably the most preferred. The smaller crevice might have contained even more eggs had it not been prone to clog with eggs near the outside, as can be seen by considering egg distribution in vertical stacks of acrylic discs; 20% of the eggs in the 1.5-mm crevice reached Zones B and C, whereas 33% of the eggs reached Zones B and C in the 3.0-mm crevice. Small crevices increase the chances of successful hatching by providing maximum protection from small fishes and other organisms, such as crayfish, that might feed on them. But, overfilling of the crevice with eggs could lead to inadequate water circulation and embryo suffocation. In 1974 small crevices in stacks of plates left in the river for 3–5 days became packed with eggs and those near the center died; eggs in lower density in a similar location were normal.

Vertical stacks of acrylic discs (with horizontal crevices) contained 87% of the total (unadjusted) eggs (Table 1); horizontal stacks (crosscurrent) with vertical crevices parallel to the current were the next most preferred and contained 7% of the eggs. Horizontal stacks with vertical crevices perpendicular to the current were the least preferred.

Fast water (0.57 m/s) had a profound effect on spawning fish. It caused them to avoid the current and to spawn on the downstream half of the discs in vertical stacks (Fig. 2). Fish may have been able to swim more easily in moderate currents (0.45 m/s) and deposited eggs over the entire disc, placing most eggs (61%) on the downstream half. In slow currents (0.23 m/s) the upstream half of the discs contained 69% of

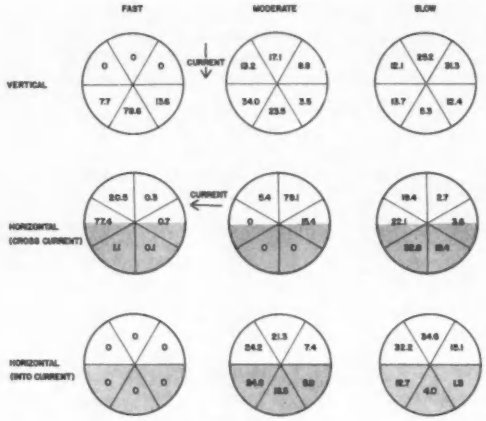

FIG. 2. Deposition of eggs on experimental plates as affected by alignment of the artificial spawning structures with current. Location of eggs is shown as a percent of the total count. Lower halves of the horizontal structures are shaded.

the total eggs, whereas the downstream portion contained the most silt and particulate iron. On horizontal stacks, where crevices paralleled the current, fish in fast and moderate currents tended to spawn on the upper portions of the stack; in slow water they spawned over the entire disc. Fish did not spawn at all on horizontal stacks (headed into the current) in fast water, where they would have had to turn broadside to the current to spawn.

The depth to which eggs were deposited within crevices was inversely related to current velocity (Table 1). In fast current, only 16% of the eggs reached Zones B and C (in vertical stacks), whereas 60% reached Zones B and C in slow current. At least two factors may have contributed to this difference. First, greater turbulence in fast water may have swept eggs against the discs before they could reach Zone B and second, more restricted spawning in fast water caused complete filling of the crevice in Zone A, preventing many eggs from passing inside.

In the five trials, only two eggs were collected on clear acrylic discs. Clear acrylic may have been nearly invisible to spotfins; Casselman and Harvey (1973) found that clear acrylic traps were efficient at catching a variety of fishes, including cyprinids and attributed the trap's success to its "invisible nature." The fact that fish did not spawn on the clear acrylic is important, for it demonstrates that vision is involved in spawning-site selection.

About 90% of the 37,815 eggs collected on vertical discs in experiment A were obtained on the upper surface of the discs forming the lower boundary of the crevices. This fact probably means that spotfins direct their eggs downward during spawning, but some eggs might have settled on the lower plate due to the gravity.

In tests to see which angle size would be preferred, spotfins spawned most frequently in the small angular (acrylic) crevices (Table 3) depositing eggs in the 15° crevice on at least eight occasions (mean 895 eggs) and in the 30° crevice 4 times (mean 147 eggs). Eggs were never found in crevices with a large angle and were observed only once in the 45° crevice. These findings are supported in a general way by our underwater observations at Port Trevorton, where fish almost always selected the smallest two crevices for spawning and displayed almost no interest in the large ones. Whether the crevices were turned away from or broadside to the current appeared to have no effect upon crevice selection.

EXPERIMENT B

In experiment B, in which stacks of black acrylic plates were presented in the river at three depths simultaneously, 91% of the eggs spawned from July 15 through July 30 were deposited on the stack near the river bottom (Table 4). But from July 31 through August 15, midwater and surface stacks received much more use than before and contained 64% of the total eggs; after August 15, spawning on the bottom stack ceased completely.

Why the pattern of stack selection would change in August is not known, but it might reflect changes in fish distribution. That is, fish may have utilized the upper waters more in August than in July and consequently came into contact with upper stacks more often than with the bottom stack. The difference might also arise as a result of fish of different ages spawning at different times. Lewis and Gunning (1959) re-

TABLE 3. Effects of angular position of artificial spawning structures (black acrylic strips) on their utilization by the spotfin shiner (July 24–August 20, 1975; only those days on which eggs were collected on the device were included in calculations of the means).

Angle	Frequency of occurrence	Egg number	
		Mean	Max
15°	8	895 ± 545	1,534
30°	4	147 ± 234	657
45°	1	3 ± 7	20
60°	0	0	0
75°	0	0	0
90°	0	0	0

TABLE 4. Effects of depth and turbidities (means of six weekly observations) on utilization of artificial spawning structures (stacks of black acrylic discs) by the spotfin shiner. JTU, Jackson Turbidity Units.

	(July 15–31)		(July 31–Aug. 16)		(Aug. 16–20)	
Turbidity (JTU)	39		50		75	
Total eggs	13,088		266,107		11,456	
	Frequency of occurrence	% Total	Frequency of occurrence	% Total	Frequency of occurrence	% Total
Stack location						
River surface	1	1.5	16	41.6	5	79.6
Midwater	4	7.2	10	22.5	4	20.4
River bottom	7	91.4	14	35.8	0	0

TABLE 5. Utilization of artificial spawning structures (stacks of acrylic plates) by the spotfin shiner from July 10 to August 20, 1975. Temperature means are based on daily values taken at 1200.

		% total no. of eggs								
	Total eggs	July 10–14	15–19	20–24	25–29	July 30–Aug. 3	4–8	9–13	14–18	19–20
Black plates	19,387	—	0.1%	1.4	2.2	19.5	44.4	23.8	6.2	2.4
Colored plates	25,587	10.0%	2.0	6.8	0	6.5	68.5	3.1	3.2	0
Water temp (C)		24.4	24.5	25.3	24.5	26.3	25.8	23.0	23.3	22.5

ported that 1-yr-old steelcolor shiner (*N. whipplei*), a species closely related to the spotfin, spawned in late August or early September and 2-yr-old fish spawned in July. Why fish of different ages should select different spawning sites is also puzzling. Yet, another possibility is that increased spawning activity in early August led to competition over spawning sites causing some fish to spawn on second or third choices of stacks. Spawning intensity was at a maximum in early August when large numbers of eggs were found on black and on colored stacks of plates (Table 5). Such an explanation, however, does not account for the lack of spawning on plates near the bottom in late August when few fish were spawning.

Because of continual mixing of water in the channel, there was almost no daily difference in the chemical and physical characteristics of the bottom and surface waters that would account for the change in spawning-site selection. But because of increased particulate iron in August, there was a pronounced increase in turbidity at that time (Table 4), and reduced visibility near the bottom may have made it impossible for the fish to see crevices in the bottom stack of plates (during periods of high turbidity scuba divers sampling in the channel sometimes found bottom waters "totally dark"). The fact that spawning on colored plates in the channel (Table 5) dropped sharply, from 68% to 3% of the total, during the period when turbidity increased from 43 to 57 JTU supports the above possibility; more support comes from observations in 1974 when artificial spawning devices were kept in the river from May through August. The devices included nylon-string mop heads near the river bottom, at midwater, and near the surface. Spotfin eggs were found on mop heads only twice, both times on the surface mop in August.

No particular crevice seemed to be preferred to the others in any of the three stacks in experiment B. Eggs were most widely distributed in the stack of plates near the bottom, where water currents were mild; on midwater and surface stacks, where water currents were stronger, fish almost always spawned on the posterior portions of the stacks, where they were sheltered from the current.

EXPERIMENT C

Examination of colored plates in experiment C at 2-h intervals permitted determination of spawning time (Table 6). Most spawning occurred between 0600 and 1000; frequency of occurrence

TABLE 6. Spawning by the spotfin shiner as related to time of day, based on occurrence of eggs on stacks of colored plates at 2-h intervals from July 11 through 31.

Time	Frequency of occurrence	Egg no.	
		Mean	Max
0600–0800	4	150±498	2,174
0800–1000	6	62±128	481
1000–1200	1	10± 42	182
1200–1400	3	47±145	599
1400–1600	0	0	0
1600–1800	0	0	0
1800–2000	0	0	0
2000–0600	0	0	0

was the greatest between 0800 and 1000, but the mean and maximum number of eggs were highest between 0600 and 0800. At Port Trevorton, spotfins were observed to begin spawning shortly after dawn, perhaps when there was sufficient light for the fish to detect suitable crevices; spawning nearly ceased by 1100. Afternoon and evening observations were not made. Stone (1940) found that *N. analostanus* spawned between 0600 and 1730 and only on sunny days.

Although no eggs were collected on colored plates between 1400 and 0600, spawning can occur during this period; on July 17, several thousands of eggs were deposited between 1630 and 1800, on a stack of black acrylic plates near a weed bed, in about 30 cm of water. One might speculate that spawning in such shallow water normally occurs in late afternoon, instead of in the morning. But, a stack of plates in the same location was spawned on the next morning between 0600 and 0630 and was not spawned on that afternoon or evening.

Near Berwick, the river substrate is heavily coated with ferric compounds which fill many, perhaps most, of the crevices suitable for spawning; as a result, there may be a shortage of high quality spawning sites. If spawning sites are in "demand," the appearance of a stack of acrylic plates, with its abundance of spawning crevices, might provide a sufficient stimulus to elicit spawning by ripe fish during a period they normally would not spawn. We observed that acrylic plates placed into an area where they had not been recently used collected large numbers of eggs for 1 or 2 days; after that, spawning frequency and mean egg number diminished. Pflieger (1965) concluded that there was a shortage of natural spawning sites in some Ohio streams because of the intensive spawning that occurred on logs he placed in the water.

In experiment C, spotfins displayed a marked preference for crevices between blue and between black acrylic plates; each contained eggs on 25 occasions (Table 7). This does not mean, however, that the crevice between the blue plates was selected for spawning 25 times. Actually, a great many spawning passes were needed to deposit large numbers of eggs in a crevice and each of these spawning passes entailed the selection of a particular crevice.

A total of 46,328 eggs was collected on colored plates; 55% of the total (mean 746 eggs) was placed between each set of blue plates and 40% (mean 547) between black plates. Crevices between white, yellow, and orange plates contained the fewest eggs, sometimes only one; such eggs may have landed there accidentally when fish were depositing eggs in a nearby crevice. Although it appears that crevices were selected because of a preference for certain colors, they were also possibly selected because of small differences in light intensity within the crevice. Crevices between dark plates would be darker than those between light-colored plates.

IMPORTANCE

The spotfin is widely distributed in North American lakes and rivers, ranging from New York and southern Quebec west through the Great Lakes to North Dakota and south to Alabama (Scott and Crossman 1973). Bunting and Irwin (1963) rated the spotfin a "poor test animal" because they "eat poorly," are "excitable in test containers," and are "difficult to identify in the field." We have not had similar problems with laboratory-reared spotfins. We think that the species has considerable potential as an organism for use in bioassay and other experiments because of its wide distribution, the ease with which large numbers of eggs can be collected on artificial spawning devices over a comparatively long period of time, and the fact that larvae eat commercially available fish food; also, it spawns early in the day, leaving plenty of time to collect and

TABLE 7. Effects of color on spawning site selection by the spotfin shiner (experiment C).

Color of plates forming crevice	Frequency of occurrence	Max no.	% Total
Blue	25	3,868	54.7
Black	25	5,820	40.1
Green	16	480	4.2
Red	12	172	0.6
White	10	30	0.1
Yellow	10	34	0.1
Orange	8	24	0.1

to process its eggs. Stone (1940) reported that both *N. analostanus* and *N. spilopterus* were easily stripped when ripe.

Lewis and Gunning (1959) have suggested that the steelcolor shiner has potential as a bait species; the spotfin might offer the same advantages, because of its great biological resemblance to the steelcolor shiner (Trautman 1957). The spotfin's bright colors and hardiness should make it an ideal bait minnow (Evermann and Clark 1920; Hubbs and Cooper 1936). Stone (1940) found that both *N. analostanus* and *N. spilopterus* were easily propagated in small ponds when brush and logs were placed in them as spawning sites. Because of Trautman's (1957) observation of the steelcolor shiner spawning on the underside of a log, Lewis and Gunning (1959) recommended the use of spawning boards in its culture. Actually, the minnows Trautman observed may have been seeking crevices in or under the bark and spawning devices containing crevices might be as desirable in the culture of steelcolor shiners as they would be in spotfin culture.

Where the spotfin is abundant it is probably an important forage fish for many sizes of game fishes; the adults are small enough to be eaten by medium-sized smallmouth bass (*Micropterus dolomieui*). Also, the spotfin's extended breeding season helps maintain a continual supply of small forage throughout much of the summer and fall.

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Significance of the Timing of Initial Feeding in Hatchery Rainbow Trout, *Salmo gairdneri*

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TWONGO, T. K., AND H. R. MACCRIMMON. 1976. Significance of the timing of initial feeding in hatchery rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 33: 1914–1921.

The age of initial food ingestion and the influence of age at initial food presentation on alevin food intake, survival, and subsequent growth were determined for rainbow trout, *Salmo gairdneri*. Alevins did not show any ingestive behavior nor was any food found in their gut, before initiation of swim-up. The withholding of food from the young fish for some time after swim-up did not impair their ability to learn to feed. Further, the most satisfactory time to initiate exogenous feeding of hatchery fish is when yolk reserves have been completely absorbed, bearing in mind that a considerable quantity of yolk may yet remain in the abdominal cavity after the externally visible yolk sac has disappeared.

This study contradicts the hypothesis that delayed feeding of young rainbow trout causes or enhances the likelihood of nonfeeding.

TWONGO, T. K., AND H. R. MACCRIMMON. 1976. Significance of the timing of initial feeding in hatchery rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 33: 1914–1921.

Nous avons déterminé l'âge auquel la truite arc-en-ciel, *Salmo gairdneri*, commence à prendre de la nourriture et l'influence de l'âge au premier repas sur l'absorption de la nourriture par les alevins, la survie et la croissance subséquente. Les alevins ne manifestant aucun comportement de prise de nourriture et leur tractus digestif ne contient aucun aliment avant le début de la nage vers le haut. Le fait de priver les jeunes de nourriture pendant quelque temps après le début de la nage vers le haut ne diminue pas leur capacité d'apprendre à se nourrir. Nous avons constaté en outre que le meilleur temps pour commencer à nourrir les poissons de pisciculture était après complète utilisation des réserves vitellines, se rapelant qu'une forte quantité de vitellus peut être encore présente dans la cavité abdominale après disparition de tout signe externe de la vésicule. Ces résultats contredisent l'hypothèse qu'un retard à nourrir les jeunes truites arc-en-ciel soit la cause ou augmente la possibilité qu'elles ne se nourrissent pas.

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UNDER natural conditions, year-class strengths of fish often appear to be established by mortality occurring early in their life history (Hjort 1926; Needham 1947; McNeil 1968; Bagenal and Braum 1971). Transition to active feeding is probably the most critical stage in the survival of young fish (Blaxter 1966; Braum 1967; Rosenthal and Hempel 1970). That this transitional phase is often critical in fish culture was first reported in North America during the late 19th century with the advent of artificial salmonid propagation (Green 1878; Porter 1878; Thomas 1879). Alevin starvation at the stage of transition to exogenous feeding as a result of their refusal to take the food provided was a recognized problem and consequently, the best food and the most opportune time for initial feeding became subjects of great concern.

The earliest school of thought proposed that the initial feeding of hatchery-reared fish should commence at the first filling of the swimbladder, i.e. swim-up (Atkins 1905). Henshall (1904, 1907) put forward a slightly different concept when he suggested that the feeding of hatchery fish should start when yolk was still present, on the assumption that wild fish under natural conditions utilize external food to supplement yolk reserves. The subsequent indication that wild alevins of some Pacific salmons feed while still utilizing yolk, and even before they achieve neutral buoyancy (Salo and Bayliff 1958; Disler 1960; Dill 1967; Thomas and Shelton 1968), is of considerable interest with respect to considerations of the most suitable time to initiate external feeding in hatchery fish.

With the exception of several studies on the feeding of young Pacific salmons (Palmer et al. 1951;

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Dill 1967; Marr 1965; Hurley and Brannon 1969; Robins and Bilton 1971; Bilton and Robins 1973), few, if any, other experiments have been designed to examine the initial feeding and subsequent feeding behavior of salmonids. Absence of published information on this aspect of the biology of the genus *Salmo*, excepting the work of Atkins (1905, 1906), is surprising in view of the large-scale alevin mortality and/or stunting that commonly occurs in trout hatcheries (Menzies 1949).

The present paper reports part of a study designed to examine the development of feeding in the hatchery rainbow trout, *Salmo gairdneri*. This part of the study consisted of a series of experiments aimed at determining the age of initial food ingestion and the influence of age at initial food presentation relative to the stage of yolk absorption on alevin food intake, survival, and subsequent growth.

The study has been focused on determining the best time to initiate young rainbow trout to external food and on testing the hypothesis that nonfeeding at the stage of transition to exogenous feeding is induced by delayed supply of food.

Materials and Methods

Rainbow trout were obtained from the Provincial Government Fish Hatchery at Normandale, Norfolk County, Ontario. The embryos were collected at the eyed stage and transferred to the University of Guelph where they were hatched in nonrecirculated well water at 8.5 ± 0.5 C and oxygen concentration ranging between 8.0 and 9.5 ppm. The chemistry of the water supply used has been adequately detailed by Hodson (1974).

Yolk Absorption and Initial Exogenous Feeding

About 1500 eleutheroembryos (Balon 1975) were used in this part of the study. Young fish were transferred 1 day after 50% hatch to small rectangular gravel-free tanks 76 × 23 × 20 cm deep supplied by well water. Oxygen concentration varied between 6.5 and 8.0 ppm. Illumination was provided by two sets of 40 W fluorescent lights (cool white) suspended 190 cm apart and 65 cm above the tanks. As the eleutheroembryos are photophobic for a number of days after hatching, sheets of translucent plexiglass 3.5 mm thick were placed on top of each tank to diffuse the light, giving an average intensity of 185 (100–250) lx (lm/m^2) at the water surface. A 12-h light–dark photoperiod was maintained.

Seven samples of 15 fish each were drawn every 4 days and placed in 10% Formalin to harden the yolk. After the alimentary track had been examined for contents, the yolk was separated from the rest of the fish and dry weights of fish were determined in the seven groups by air drying to constant weight at 110 C (Brett and Higgs 1970; Brett 1971). Live brine shrimp larvae, *Artemia salina*, and commercial feed (EWOS trout starter) were made available to the eleutheroembryos at day 15 (from hatching) when they showed increased activity, including momentary excursions off the aquarium bottom.

Initial Food Presentation, Food Intake, and Subsequent Growth

Two days after all embryos had hatched, five samples of about 350 eleutheroembryos each (hereafter designated Group 1, 2, . . . 5) were transferred to five rearing tanks similar to those described previously. Conditions of water temperature, water chemistry, and illumination were as described previously. Feeding of the five groups with brine shrimp larvae and EWOS starter feed was initiated at days 21, 28, 35, 42, and 49 (after hatching), respectively. Day 21 was selected for the first feeding of Group 1 as no alevins had been noted to ingest food before that time in preliminary experiments.

Throughout the rearing period, samples of 11 fish from each of the five groups were tested for food intake every 6 days beginning on day 22 when about 50% of the alevins had achieved neutral buoyancy. Food intake tests were done in separate tanks 25 × 23 × 20 cm deep, each with a separate inflow controlled by a tap, an air stone, and an outflow. Water conditions and illumination were similar to those of the rearing tanks. Prior to the test, the fish were deprived of food for 72 h to facilitate complete evacuation of the alimentary tract by the groups that had already been initiated to food (Windell et al. 1969, 1972; Tyler 1970; Brett 1971). Water flow in all test tanks as well as aeration were adjusted to be as similar as possible to minimize differences in exertion due to turbulence.

Each group was tested on shrimp larvae and starter feed separately. A food-intake test lasted 15 min during which time the alevins were given excess food. The duration of 15 min was determined during preliminary experiments to be the average period of feeding time after which shrimp larvae passed into the intestine from the stomach. The starter feed took much longer than 15 min. Immediately after the test period the fish were quickly killed and preserved in 10% Formalin. Total length of each alevin was measured to the nearest millimeter using a vernier caliper. Alevins were then dissected and the stomachs examined for fullness at 25 × magnification. Each stomach was assigned one of five indices of fullness (0–4) as an estimate of the amount of food ingested. A completely empty stomach received an index of 0 and a stomach that was well distended with food from the cardiac to the pylorus and felt taut to the touch of a dissecting needle was assigned an index of 4. By definition, index 1 was extended to include mere presence of food in the stomach. However, in practice most of the alevins that ingested food at all, often took more than just a trace. Assignment of the intermediate indices of stomach fullness was refined after examining well over 1000 stomachs by a single observer during preliminary investigations. It was based on the proportion of total stomach volume that

contained food. Food contained in stomachs was clearly visible owing to the translucent nature of the stomach wall and the color of shrimp larvae (pink) and EWOS starter feed (reddish). The sample dry weight for each group of alevins was determined after air drying to constant weight at 110 C.

Food-intake tests were terminated at day 78. At day 103 all the alevins remaining in each group were killed and measured for total length. The alevins in each of Groups 1–4 were subsampled into five lots of 10. Group 5 which had only 34 specimens was divided into four subsamples of seven fish and one of six. The dry weight of the samples was obtained as described above. Termination of the experiment after 103 days was prompted by the appearance of some unidentified infection amongst Group 2 fish causing them not to feed for a day. The experiment had been scheduled to end after 120 days.

Results

Yolk Utilization and Initiation of Exogenous Feeding

Half of the alevins achieved neutral buoyance on day 22 when 88% of the original yolk at hatching had been used up (Fig. 1). Food (brine shrimp larvae) was first recorded in the stomachs of the alevins on day 21 when about 25% of them had achieved neutral buoyance. Only the alevins that had achieved neutral buoyance ingested food, and at this age 90% of them had food in their stomachs ($n = 100$). A day later when 50% swim-up was recorded, only 44 of the free-swimming fry ingested the starter feed ($n = 50$). Although both foods were made available from day 15 when the eleutheroembryos showed increased activity including momentary excursions off the aquarium bottom, no food was found in their alimentary canal before attainment of neutral buoyance. At swim-up the parr marks were clearly visible, the fin fold had completely disappeared, and the median fins were fully formed. On day 29 about 19% had used up their yolk reserve ($n = 105$), while 4 days later 75% had no solid yolk left ($n = 105$). Complete absorption of solid yolk in all samples occurred at about day 35.

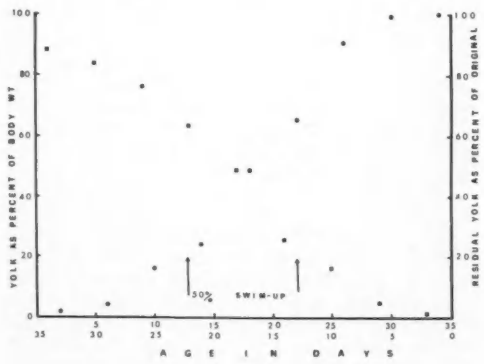

FIG. 1. Rate of yolk absorption of the eleutheroembryos of the rainbow trout, *Salmo gairdneri*. ■, Residual yolk as percent of body weight; ●, Residual yolk as percent of quantity at hatching.

Food Intake and Growth

Previous history of feeding had little apparent effect on feeding response of alevins to either shrimp larvae or hatchery feed. Food intake data are shown in Fig. 2 where indices of stomach fullness are plotted for the five test groups. Change in shrimp larvae intake followed basically the same pattern regardless of age at initial feeding. There was an initial increase in intake until about day 35 followed by fluctuating values which in experimental Groups 3, 4, and 5 tended to rise to a slightly higher maximum value than that recorded during the initial increase. Increase in the intake of starter feed was more gradual and lacked the initial peak shown for shrimp larvae. However, analysis of the indices of stomach fullness for the effect of food type over age showed significantly higher intake for shrimp ($P \leqslant 0.05$) only on test days 28 and 34. There was no significant difference in food intake on day 22 and after day 35. A multivariate analysis of variance was applied at $P \leqslant 0.01$ to make it more conservative since data were analyzed age by age.

Initial exposure to external food induced an increase in food intake of both foods regardless of the age at which it was done. For example Group 3 alevins, which were exposed to food initially at age 35 days, showed an increase in food intake during the next test on day 40. Similarly Group 4 alevins showed increased food intake on day 46 following their initial exposure to food on day 42. The initial peak in food intake referred to above was much higher in Groups 1 and 2 which were initiated to external food well before the increase reached the peak about day 35. Although fish that had previously received food almost always scored higher food intake values on a given test day than the ones that had not, the differences were not significant. An analysis of the effect of age and previous feeding experience on the food intake of alevins is presented in Table 1. Food intake of alevins that had no previous feeding experience did not increase significantly between days 22 and 46 (the period of food deprivation). Similarly, that of alevins having previous feeding experience did not change

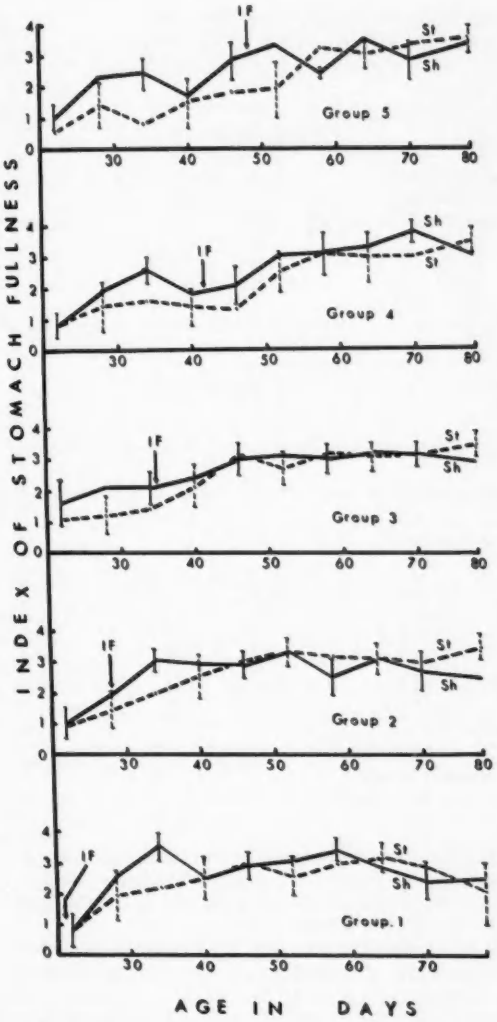

FIG. 2. Effect of food type and age at initial exposure to food in alevin rainbow trout, *S. gairdneri*. Initial feeding (IF) of shrimp larvae (Sh) (———), and starter feed (St) (– – – –). Vertical lines indicate 95% confidence intervals.

significantly between days 28 and 46; however, all the food intake values of prior experience alevins on day 22 i.e. before exposure to food, are significantly lower than at any subsequent age ($P \leqslant 0.01$).

Alevins deprived of food the longest were also the smallest. Alevins from Groups 3, 4, and 5 actually were losing weight when food was initiated. However, positive growth was recorded as soon as food was made available. The mean length and weight of groups first initiated to food were consistently higher than those of groups receiving food later, except for Group 2 whose mean weight overtook that of Group 1 at about day 74, and by day 78 the mean length of Group 2 fish was higher than that of Group 1 (Table 2). Rates of increase in dry weight of Groups 3, 4, and 5 (see slopes of regression equations Fig. 3) were similar and they were the highest, although they did not differ significantly from that of either Group 1, which was the lowest, or that of Group 2 ($P \leqslant 0.01$). Although the rates of increase in length of Groups 2 and 3 (Fig. 4) were not significantly higher than that of Group 1, they were the highest recorded. There was no decrease in mean length of any of the starved groups of fish as was reported for sockeye salmon (*Oncorhynchus nerka*) (Paine 1971; Bilton and Robins 1973). An apparent decrease in mean length of fish used in a preliminary experiment was recorded because the larger alevins tended to die off first, mainly as a result of an infestation by *Costia* sp.

The final growth data (Table 3) show that the mean weight of Group 2 was lower than that of Group 1. However, before the outbreak of infection it was quite obvious to the observer that the fish in experimental Groups 2 and 3 showed the best condition, appetite, and uniformity in size. Group 1 fish were most variable in size, consisting of some large healthy looking fish together with small lean ones. The final size distribution of the alevins in the five experimental groups at age 103 should be compared with that on day 60 when the effects of starvation were still marked in the groups initiated to food last. The coefficient of variation in mean length (Table 3) and the 95% confidence intervals about the mean lengths illustrate the variability in size. Statistical comparison of the growth data using Duncan's multiple-range test showed that only the mean lengths of experimental Groups 1 and 2 did not differ significantly. The mean weights of all the groups were significantly different from one another ($P \leqslant 0.05$).

ALEVIN MORTALITY

Alevin mortality increased with the duration of food deprivation prior to initial feeding (Table 4). Hence experimental Group 1 suffered the lowest mortality while Group 5 suffered the highest. The mortality of the groups deprived food longer than day 35 after hatching tended to increase sharply following initial food presentation.

TABLE 1. Effect of age and previous feeding experience on food intake of rainbow trout, *Salmo gairdneri*. The values given are the mean index of stomach fullness; indices were analyzed by using analysis of variance. Means were compared using Scheffe's test (Gunther 1964). Sample sizes are in parentheses.

	Had prior experience			No prior experience	
Age (*days*)	Shrimp-tested	Starter tested	Mean no. days of prior experience	Shrimp-tested	Starter tested
22	1.0[a](55)	0.8[a](55)	0	1.0 (55)	0.8 (55)
28	2.5 (11)	1.9 (11)	4.0	2.0 (44)	1.3 (44)
34	3.2 (22)	2.0 (22)	6.5	2.4 (33)	1.3 (33)
40	2.6 (33)	2.4 (33)	9.0	1.7 (22)	1.3 (22)
46	2.7 (44)	2.6 (44)	11.5	2.8 (11)	1.7 (11)

[a]Had no prior experience as fish were isolated from main batch first exposed to food on day 21.

TABLE 2. Growth data for rainbow trout, *S. gairdneri*, alevins initiated to external food at various ages. Mean lengths are given with 95% confidence limits.

	Mean length (*mm*)					Mean dry wt (*mg*)				
	Experimental Groups									
Age (*days*)	1	2	3	4	5	1	2	3	4	5
22	22.9±0.44	23.4±0.55	23.4±0.33	23.7±0.32	23.7±0.32	14.4	14.8	15.0	16.0	14.0
28	[a]24.3±0.43	23.7±0.40	24.0±0.37	24.1±0.54	24.1±0.55	14.5	13.2	14.0	13.8	12.6
34	24.7±0.33	23.9±0.57	24.3±0.47	24.0±0.44	24.0±0.44	15.2	13.2	12.8	11.2	11.4
40	25.4±0.55	25.4±0.57	24.0±0.61	24.5±0.59	24.5±0.58	14.8	14.6	10.6	10.0	10.2
46	27.7±0.76	26.0±0.67	24.6±0.51	24.4±0.57	24.7±0.47	19.2	15.2	11.6	9.2	8.2
52	28.2±1.27	27.7±0.55	25.5±0.94	24.2±0.45	25.1±0.53	23.1	21.4	12.4	10.7	8.3
58	29.9±1.13	30.5±0.76	28.0±1.03	25.3±0.68	24.5±0.48	29.6	28.2	19.6	11.9	8.2
64	33.0±1.15	30.6±0.63	29.3±0.98	26.4±0.94	24.7±0.60	40.5	29.6	25.4	16.0	10.5
70	33.6±1.27	33.0±1.08	30.7±0.89	28.6±0.90	26.7±1.06	46.2	40.0	31.3	22.6	14.2
78	34.9±1.58	35.6±1.36	33.4±1.20	30.8±1.15	28.4±1.04	52.8	59.5	44.0	33.5	23.8

[a]Underlined are the values following the initial supply of external food. Only values obtained after the initiation of feeding are plotted (see Fig. 3 and 4) since main interest was in the nature of growth subsequent to initiation of food.

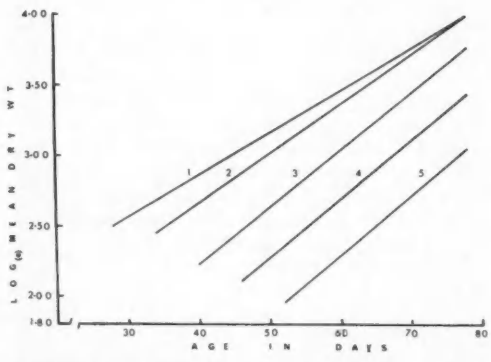

FIG. 3. Regression of $\ln_e$ mean dry weight on age of rainbow trout, *S. gairdneri*, alevins initiated to external food at various ages. Regression equations: Group 1 $\ln_e$ wt = 1.6778 + 0.0297*t*; Group 2 $\ln_e$ wt = 1.2816 + 0.0346*t*; Group 3 $\ln_e$ wt = 0.6283 + 0.0401*t*; Group 4 $\ln_e$ wt = 0.2202 + 0.0412*t*; Group 5 $\ln_e$ wt = 0.2332 + 0.0421*t*.

TABLE 3. Effect of age at initial exposure to external food on subsequent final growth of rainbow trout, *S. gairdneri*, alevins. Means are given with 95% confidence limits; C.V. is coefficient of variation.

Experimental group	Mean length (*mm*)	C.V.	Mean wt (*mg*)
1	38.0±1.37[a]	12.7	95.1±33.3
2	39.2±0.86[a]	7.7	88.2±10.8
3	40.7±0.86	7.5	133.1±12.4
4	35.2±0.60	6.0	57.0±10.3
5	32.0±0.66	5.8	29.7± 3.0

[a]The mean lengths of Groups 1 and 2 do not differ significantly ($P \geq 0.05$) according to Duncan's test.

Discussion

It is standard procedure in some trout hatcheries in Canada and the USA to provide the initial supply of food to young trout before or during swim-up (personal communication from

TABLE 4. Mortality of rainbow trout, *S. gairdneri*, alevins initiated to food at various ages. Original number of each group is approximately 350 fish.

Group	Age at first feeding (*days*)	No. dead fish in group: Age (*days*) 20–41	42–56	57–72	73–102	Total no. dead	Mortality (%)
1	21	0	0	0	2	2	0.6
2	28	3	1	0	3	7	2.0
3	35	3	4	1	2	10	2.9
4	42	4	24	2	3	33	9.4
5	49	4	35	4	4	47	13.4

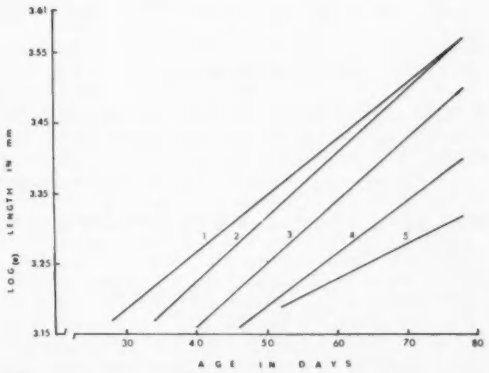

FIG. 4. Regressions of $\ln_e$ length on age of rainbow trout, *S. gairdneri* alevins initiated to external food at various ages. Regression equations: Group 1 $\ln_e$ length = 2.9410 + 0.0080*t*; Group 2 $\ln_e$ length = 2.8628 + 0.0090*t*; Group 3 $\ln_e$ length = 2.7977 + 0.0090*t*; Group 4 $\ln_e$ length = 2.7999 + 0.0077*t*; Group 5 $\ln_e$ length = 2.9269 + 0.0050*t*.

hatchery managers in Canada and the USA). Results of this study indicate that alternative management practices may be preferable.

The age (21 days) at which food was first found in the stomachs of young rainbow trout in gravel-free environment does not differ much from 16 days for rainbow trout at 10 C reported by Brown and Buck (1939). Although their study does not relate first feeding with swim-up, alevins were not observed during the present study to show any ingestive behavior nor was any food found in their gut before initiation of swim-up. Then, the intestine was still full of the yellowish green bile-like substance typically found in eleutheroembryonic intestines. The substance was "washed out" when the young fish swallowed air and water during the process of swim-up. Further, evidence from a histological study (Twongo 1975) showed that the upper alimentary tract of young rainbow trout used in the study was completely occluded by a tissue plug until several days before swim-up. It is, therefore, unlikely that presentation of food to young rainbow trout before the onset of swim-up is of any advantage. Such early supply of food could, in fact, cause water fouling problems that might be accompanied by oxygen depletion and disease.

There was no evidence to suggest that making food available to the young fish during swim-up provided them with early experience that was advantageous during the early stages of development of feeding. Group 1 fish, first fed during swim-up, did not sustain higher food-intake values than the other groups initially fed subsequently. Data analysis summarized in Table 1 shows that after the initial experience with food, the young fish in any group scored food-intake values comparable to those scored by groups that had earlier exposure to food. Data indicate that feeding behavior does not develop gradually with age over a long period of time but appears to occur suddenly, its manifestation as food intake being stimulated by the initial exposure to food. The latter inference is illustrated graphically (Fig. 2) by the sudden rise in food intake a few days following initial exposure to food. The persistence of this initial response to food (though comparatively low) as late as 24 days after swim-up (day 46, Fig. 2, Group 5) would likely serve as a useful adaptation to environments where food supply may not be available at the time the alevins first require it.

Probably the clearest indication of the most suitable time to initiate the feeding of rainbow trout is to be found in the final growth data (Table 3). Group 3 fish initially fed on day 35 (over 10 days since swim-up) showed the highest final mean weight and length of 133.1 mg and 40.7 mm, respectively. Groups 2 and 3 showed

the best appetite throughout the rearing period and the latter group of fish (first fed on day 28, 6 days after swim-up) attained the next highest final mean length. Further, Groups 3, 4, and 5 (the last two groups were fed even later than 35 days after hatching) showed the most rapid rate of weight gain (Fig. 3) implying the best food ingestion and/or utilization. These results corroborate the findings of Bilton and Robins (1973) who reported that sockeye salmon alevins deprived of food for 1–3 wk caught up to the control group by the end of 8 wk. In contrast, Hurley and Brannon (1969) found no significant difference in rate of weight gain between the starved and control groups of sockeye salmon.

Group 3 fish, which recorded the highest growth, were initially fed on day 35 when their yolk reserves were virtually exhausted. In this regard the stage of yolk utilization appears to be a useful visual guide to the best time to initiate feeding young rainbow trout, bearing in mind that considerable quantity of yolk may yet remain in the abdominal cavity after the externally visible yolk sac has disappeared. The observed occurrence of the most uniform size of fish within previously starved test groups (Table 3) is worthy of some thought, especially in consideration of the caution expressed by Hurley and Brannon (1969) against the assumption that feeding, prior to yolk absorption, gives young sockeye salmon a good start and greatly decreases the occurrence of stunted or pinhead fry. The present study reveals conclusively that those rainbow trout alevin fed earliest were most variable in size and contained more stunted fish than those that first received food at a more advanced age.

Although alevin mortality increased proportionately with the period of food deprivation (Table 4), there was no marked difference in the mortality of the five groups until after day 35, thus indicating that starving the fish to that stage does not significantly increase mortality. Similar mortality pattern was reported by Atkins (1906), Paine (1971), and Bilton and Robins (1973). Therefore, withholding food from young trout for some time after swim-up until all yolk reserve is absorbed, apparently does not only facilitate initiation of feeding when the fish are most responsive to food and have fairly uniform appetite, but it promotes more efficient food utilization and growth.

Results of food deprivation experiments do not support the hypothesis that delayed initiation of feeding induces nonfeeding. Fish deprived of food until 35, 42, and even 49 days after hatching scored similar intake values to the control group only a few days after food had been made available (Fig. 2). Further, growth rates of the alevins first fed on days 28, 35, and 42 were similar and the highest. These observations corroborate growth data reported for brook trout (*Salvelinus fontinalis*), Atlantic salmon (*Salmo salar*) (Atkins 1906), and sockeye salmon (Bilton and Robins 1973). No doubt, starvation from a lack of available food will ultimately lead to a weakened condition whereby feeding becomes impossible even when suitable food becomes abundant. Indeed, during preliminary experiments alevins starved beyond day 49 failed to feed subsequently. But at that stage the alevins apparently did not simply refuse to feed, they had reached the "point of no return" (Blaxter 1965), the point after which the young fish are still living but too weak to take food.

Acknowledgments

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Molt- and Growth-Enhancing Effects of Bilateral Eyestalk Ablation on Juvenile and Adult American Lobsters (*Homarus americanus*)

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MAUVIOT, J. C., AND J. D. CASTELL. 1976. Molt- and growth-enhancing effects of bilateral eyestalk ablation on juvenile and adult American lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 33: 1922–1929.

Growth rate of 20 juvenile lobsters (*Homarus americanus*) at the 7th or 8th stage (2 mo old) and 9 older juveniles (5 mo old) was greatly enhanced by bilateral eyestalk ablation. The average weight of 7th and 8th stage ablated lobsters was 5 times that of controls 200 days after the operation. This increased growth was the result of increased molt frequency and greater percent weight gain per molt. Dietary composition was more critical to the survival and growth of the ablated lobsters than it was to the controls. A low protein diet resulted in reduced growth and survival of ablated lobsters but had little effect on controls. Biochemical analyses revealed that although the fast growth of ablated lobsters resulted in decreased lipid deposition in whole tail, chelae, and hepatopancreas, the faster growth rate was the result of real tissue synthesis and protein deposition.

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L'ablation bilatérale du pédoncule oculaire a pour effet d'accélérer considérablement le rythme de croissance de 20 homards américain juvéniles (*Homarus americanus*) aux 7^e ou 8^e stades (âgés de 2 mois) et de 9 juvéniles plus âgés (5 mois). Deux cents jours après l'opération, le poids moyen des homards opérés aux 7^e et 8^e stades est 5 fois plus grand que celui des témoins. Cette augmentation de croissance est le résultat d'une augmentation à la fois de la fréquence des mues et du gain pondéral en pourcentage par mue. La composition du régime alimentaire est un facteur de survie et de croissance plus critique chez les homards opérés que chez les témoins. Un régime pauvre en protéines entraîne une diminution de croissance et de survie chez les homards opérés, mais affecte peu les témoins. Des analyses biochimiques démontrent que, bien que le rythme de croissance des homards opérés résulte en une déposition moindre des lipides dans la queue entière, les pinces et l'hépatopancréas, le rythme de croissance accéléré est le résultat d'une réelle synthèse tissulaire et d'une déposition de protéines.

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THERE have been conflicting reports on effect of eyestalk ablation in the American lobster, *Homarus americanus*. Flint (1972) observed that ablation appeared to lengthen the intermolt period in adult lobsters. Sochasky et al. (1973) and Rao et al. (1973), however, found that eyestalk ablation increased the molt rate in lobsters. Neither of these authors report lobsters molting more than twice after ablation.

Diet may play a significant role in the survival of eyestalk-ablated animals. Smith (1940) reported 100% mortality for eyestalk-ablated crayfish (*Cambarus clarkii*) that were only "very lightly fed." When a second group was fed liberally, however, he found 22 of 45 ablated animals successfully molted twice and three molted a third time. Rao et al. (1973) fed their lobsters guppy food. Sochasky et al. (1973) did not report what their lobsters were fed.

In this study, effects of eyestalk ablation on juvenile and adult lobsters are further investigated. This report deals with comparison of growth and several other physiological factors for eyestalk-ablated and control lobsters. The effect of diet is also evaluated.

Materials and Methods

Larval lobsters were hatched from gravid females as described previously (Castell et al. 1975). Larvae were hatched September 10–13, 1974 and held (100–1000 larvae) in 136-liter rectangular fiberglass aquaria, supplied with filtered 20 C sea water. Larvae

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were fed newly hatched brine shrimp (*Artemia salina*) in these tanks until they reached the 4th stage. Water was aerated with air stones and changed every 2nd or 3rd day. All lobsters reached 4th stage by September 20–October 5, at which time they were transferred to plastic trays with individual compartments to prevent cannibalism. Trays were supplied with continuous-flowing 20 C filtered sea water. All juveniles were fed ad lib. on frozen adult brine shrimp (FBS) every day except where noted. Excess food and waste were siphoned out of the trays every morning before feeding.

Adult lobsters were obtained locally in November, 1974, held at ambient temperature (1–9 C), and fed beef liver and herring on alternate days until experiments were initiated in April 1975.

Experiment 1

On December 17, one eyestalk was removed with a small pair of dissecting scissors from 20 of the juvenile lobsters which were in the 7th or 8th stage. On the following day the second eyestalk was removed in the same way. Thirteen juvenile lobsters were held as unoperated controls. Ablated and control lobsters were fed ad lib. on FBS from December 18, 1974 until March 11, 1975. On March 11, the surviving lobsters from each group were subdivided as shown in Fig. 1. Composition of Diets 1 and 2 is given in Table 1. Raw fisheries products were passed through a Hobart meat grinder, then thoroughly mixed. The mix was cooked in an autoclave for 5 min at 15 lb/in.^{2} (10,546.5 kg/m^2) and 120 C. After the food had cooled and gelled in a refrigerator for several hours, it was cut into small pieces and frozen at −20 C until fed to the lobsters. This second feeding program was continued daily, ad lib. for 55 days (from March 11 to May 5, 1975). At this time all surviving lobsters were recombined into one group and fed Diet 3 (Table 1) until termination of the experiment (July 30, 1975).

All lobsters were weighed at the beginning of the experiment and about 4 days after each molt. Carapace length of the cast shell was also measured in some cases.

Experiment 2

On February 27–28, 1975 nine juveniles from the same female as those in Experiment 1 were ablated. These juveniles as well as 8 control lobsters from the same group had been fed FBS and held at 20 C. This food and temperature regime was continued until termination on June 4, 1975. Weights were again determined about 4 days after each molt.

Experiment 3

Six commercial lobsters (500–700 g), three male and three female, were selected from the stock of animals received in November. Four lobsters were ablated on April 3 and 4 as described above. The only difference in the operational procedures was that these animals, which had been maintained in ambient sea water, were held at ambient temperature (about 1 C) until 1 wk after ablation. At this time the temperature was slowly elevated to 20 C over a 24-h period. All these lobsters were fed Diet 3 throughout the experimental period from April until July 30.

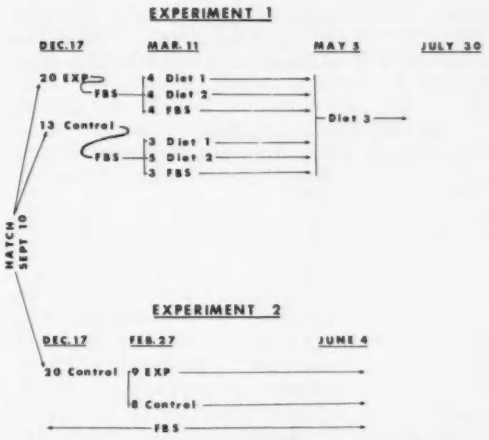

FIG. 1. Flow chart for American lobster (*Homarus americanus*) distribution in Experiments 1 and 2; Exp = eyestalk-ablated lobsters, FBS = frozen brine shrimp.

Statistical Methods

Standard deviation, standard error of the mean, linear regression and analysis of variance were calculated according to the methods described by Snedecor and Cochran (1967).

Biochemical Analysis

Three juveniles from the ablated and three from the control group of Experiment 1, and five ablated and five controls from Experiment 2 were sampled 174 and 96 days (for Experiments 1 and 2, respectively) after eyestalk removal. Serum protein, percent dry weight of lateral dorsal muscle, hepatopancreas, and tail plus chelae (including shell), and hepatopancreas glycogen were analyzed by the procedures used by Castell and Budson (1974). Percent lipid of the muscle and hepatopancreas was determined by the Bligh and Dyer (1959) method. Protein content of muscle was estimated from the nitrogen content determined by predigesting dried samples in 50% sulphuric acid and automated Kjeldall analysis (Ferrari 1960). Ashed samples of shell were predigested in 6 N HCl with a few drops of concentrated HNO_3 for calcium determination by the atomic absorption method (AOAC 1970) using a Unican Model SP-90 Atomic Absorption Spectrophotometer.

Results

Growth

Weights of ablated and control lobsters from Experiment 1 are plotted against time in Fig. 2.

TABLE 1. Composition of diets used for juvenile and adult American lobster (*Homarus americanus*) eyestalk ablation studies.

Ingredient	% in Diet			
	1	2	3	Brine shrimp
Mussel	10.0	8.0	33.3	
Squid	28.0	8.0	12.2	
Clams	16.6	5.0	—	
Oysters	8.0	—	—	
Crab	—	7.0	24.3	
Krill	—	12.0	—	
Brine shrimp[a]	—	24.0	—	
Bread	6.2	8.8	—	
Fish meal	21.3	4.0	—	
α-Cellulose[b]	4.0	8.0	2.7	
Gelatin[b]	—	8.0	5.3	
Soybean Protein[b]	—	—	6.7	
Fish protein concn	—	—	4.0	
Casein (vitamin free)[b]	—	—	5.3	
Dextrin[b]	—	—	2.7	
Agar[b]	4.4	7.2	—	
Mineral mix[b,c]	1.1	—	—	
Vitamin E[b]	—	—	0.08	
Vitamin mix [b,d]	—	—	0.80	
Corn oil[b]	—	—	1.07	
Cod liver oil[b]	—	—	1.07	
Cholesterol[b]	—	—	0.20	
Choline[b]	—	—	0.28	
Protein (wet wt)	25.85	15.14	26.0	4.2
Protein (dry wt)	64.46	27.53	64.0	41.7
Moisture	59.94	45.00	59.38	90.0

[a]Frozen San Francisco Bay brine shrimp.

[b]Ingredients purchased from ICN, Nutritional Biochemicals Corp. Most of the other materials (mussels, clams, etc.) were obtained locally.

[c]Bernhart-Tormelli modified salt mix.

[d]Vitamin mix composition as listed by Castell and Budson (1974).

The best fit polynomial curve, calculated by the least squares method for the ablated lobsters was:

$$Y = .276 + 5.11 \times 10^{-2}(x) - 1.21 \times 10^{-3}(x)^2 + 3.73 \times 10^{-5}(x)^3 - 2.97 \times 10^{-7}(x)^4 + 8.30 \times 10^{-10}(x)^5$$

where Y was the weight in grams and x the time in days. Index of determination was 0.975. For the control lobsters the best fit curve was calculated by a log regression, $\text{Ln } Y = 1.61 \times 10^{-2}(x) - 0.859$, with a correlation coefficient of 0.886. After 200 days, the ablated lobsters in Experiment 1 weighed 5 times as much as the controls. Molts and percent weight gain per molt over this period are given in Table 2. A similar result was obtained in Experiment 2 where the ablated lobsters were 3 times as heavy as the controls after 100 days (Fig. 3). Increased growth rate caused by eyestalk ablation was the result of a decrease in the intermolt period and an increase in the percent weight gain at molt.

	Exp 1	Δ	Exp 2
Ablated			
intermolt 1–2	13.5 days	(+51%)	20.4 days
% wt gain	+93.1	(−14%)	+79.9
Control			
intermolt 1–2	22.7 days	(+51%)	34.4 days
% wt gain	+71.0	(−14%)	+60.9

Ablated and control lobsters in Experiment 2 showed an increased intermolt period (51%) and a decreased weight gain (−14%) for the first molt compared with those of Experiment 1. These changes were due to the fact that Experiment 2 lobsters were older (Fig. 1). Table 2 shows that with increasing age the percent gain after molt decreases and the intermolt period increases for ablated and control lobsters.

All ablations were performed on the same days in each experiment. Lobsters were ablated at all stages in the molt cycle from immediately post-ecdysis to 1-day preecdysis. Lobsters that were beyond D_2 stage of ecdysis were much less affected than those in C stage. This is reflected in

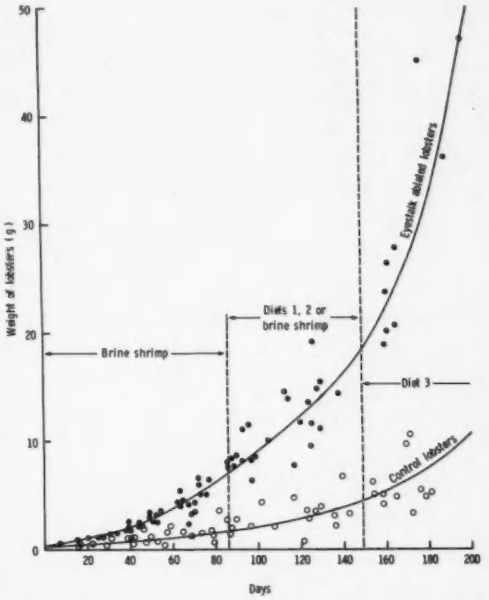

FIG. 2. Growth curves for eyestalk ablated (●) and control (○) lobsters for Experiment 1.

the mean (±SE) percent weight gain for lobsters molting less than 4 days after ablation (74.0 ± 10.3% and 58.7 ± 1.9% for Experiments 1 and 2, respectively), and those molting later than 4 days after ablation (94.3 ± 11.7% and 70.8 ± 8.2% for Experiments 1 and 2, respectively). The stage in the molt cycle at which eyestalk ablation was performed had a significant effect on the percent weight gain at molt for the first molt after ablation. By the second molt there was no significant difference in the percent weight gain relative to the stage at ablation.

The linear regression of lobster weight (grams) against intermolt period length (days) was calculated for eyestalk-ablated lobsters of Experiment 2:

$$Y = 18.1 + 0.848\,X \text{ with correlation coefficient } (R^2 = 0.943)$$

where Y = intermolt period, X = weight of ablated lobster. The mean percent weight gain for the intermolt period, 4 days postmolt to 4 days premolt for control and ablated lobsters was 9.2 ± 0.4%.

Though the number of commercial lobsters in Experiment 3 was small, eyestalk ablation did result in increased molt and greater percent weight gain than was obtained with control lobsters (Table 3). One of the four adult lobsters ablated on April 14 died after the operation; he apparently bled to death. The tissue was not cauterized after the operation and all adults bled profusely after the eyestalks were removed. A second ablated lobster died on June 3. The autopsy revealed several of the large rubber bands used to immobilize the chelae were in the stomach and prevented passage of food.

COMPOSITION OF JUVENILE LOBSTER TISSUES

A number of biochemical analyses were done on juvenile lobsters from Experiments 1 and 2 to determine whether or not eyestalk ablation and rapid weight gains had altered the composition of lobsters. Results of these tests are given in Table 4. There was no significant difference between ablated and control lobsters in the percent dry weight or protein content of muscle tissue, percent dry weight of whole tail and chelae, calcium content of shells, or glycogen content of the hepatopancreas. Control lobsters did have significantly higher whole tail and chelae lipid, hepatopancreatic percent dry weight and lipid and tended to have higher serum protein levels.

DIET

The significant result of the preliminary diet trial in Experiment 1 was that ablated lobsters

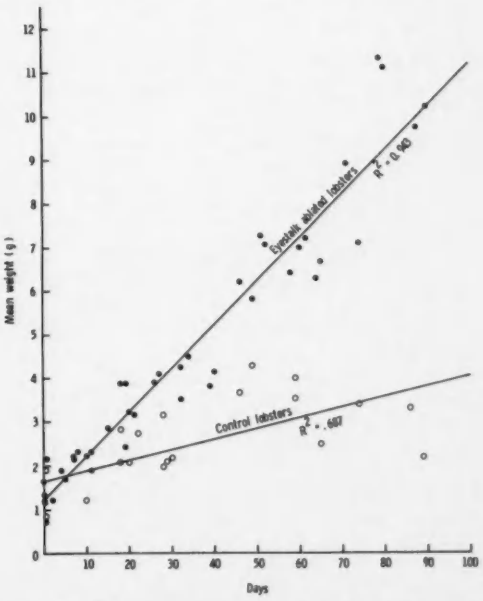

FIG. 3. Growth curves for eyestalk ablated (●) and control (○) lobsters for Experiment 2.

TABLE 2. Effect of eyestalk ablation and age on weight gain and length of molt cycle of lobsters.

No. molts per lobster	Ablated			Control		
	No. lobsters[a]	% Wt gain	Days between molts	No. lobsters[a]	% Wt gain	Days between molts
			Experiment 1			
1	18	86.3±7.7	—	13	69.7±9.3	22.7±3.4
2	18	93.1±5.4	13.5±1.4	13	71.0±9.8	22.7±3.4
3	17	88.4±7.7	16.6±1.1	13	64.6±9.8	29.5±7.7
4	16	83.5±5.1	21.4±1.8	12	65.6±7.5	31.3±5.3
5	15	86.2±4.6	22.9±1.2	10	53.7±9.7	40.0±8.1
6	14	69.5±7.5	27.3±2.5	7[b]	52.3±10.6	37.7±9.0
7	10	67.2±8.0	30.5±2.4	2[b]	35	29
8	6[b]	72.2±13.6	32.5±6.0			
9	2[b]	74.1	29.0			
			Experiment 2			
1	9	66.8±6.7		8	53.9±3.7	
2	9	79.9±8.7	20.4±2.9	8	60.9±4.4	37.4±4.7
3	9	69.5±9.4	25.6±2.0	2[b]	69.9	54
4	6[b]	50.5±16.8	27.0±2.1			

[a]Number of lobsters successfully completing number of molts indicated in left-hand column.

[b]In all cases except these, the number of lobsters successfully molting also represents the number of survivors. In Experiment 1, 8/20 ablated and 7/13 controls survived to 200 days. In Experiment 2, 9/9 ablated and 5/8 controls survived to 96 days.

TABLE 3. Effect of eyestalk ablation on adult lobsters; M = male, F = female; C.L. = carapace length.

Lobster	Initial wt (*g*)	Postmolt wt (*g*)	Wt gain (%)	Initial C.L. (*cm*)	Postmolt C.L. (*cm*)	Increase C.L. (%)	Molt date
Ablated							
No. 1 M	545	909	64.4	9.0	10.1	12.2	June 1
No. 2 F	690	1059	51.3	9.4	10.5	11.7	June 5
Control							
No. 1 F	700	813	16.1	9.5	10.5	10.5	July 1
No. 2 M	500	625	23.8	8.2	9.7	18.3	July 1

were more sensitive to dietary differences than were controls. Ablated lobsters receiving the low protein (Diet 2) had a lower mean percent weight gain per molt and a longer mean intermolt period (significance at $P = 0.05$) than the ablated lobsters receiving the high protein (Diet 1) or FBS (Table 5). Though there was no direct comparison between Diet 3 (Table 1) and Diets 1, 2, and FBS (see Fig. 1), the mean weight gain for ablated lobsters receiving this diet was 77.5 ± 7.9% for eight molts and eight lobsters. Since the percent weight gain decreases with each succeeding molt, Diet 3 was apparently superior to Diet 2.

Discussion

Though the molt- and growth-enhancing effect of eyestalk ablation on crustaceans has been known for nearly seven decades (Passano 1960; Brown and Cunningham 1939; Abramowitz and Abramowitz 1940; Smith 1940; Zeleny 1905), we are unaware of any other report of ablated animals surviving for more than three molts after ablation. Effects of eyestalk ablation have been observed on the crayfish (*Cambarus clarkii*) (Smith 1940), crab (*Eriocheir sinensis*) (Koch 1952), prawn (*Leander serratus*) (Carlisle and Butler 1956), spiny lobster (*Panulirus argus*) (Travis 1951), and other crustaceans (Passano 1960). Eyestalk ablations have always led to high mortality. Brown and Cunningham (1939) reported 100% mortality of eyestalkless crayfish (*Cambarus* sp.). Almost all mortalities occurred during or immediately after molting. Though these authors did not mention the amount or type of food used in their experiments, Smith (1940)

TABLE 4. Effect of eyestalk ablation on several physiological parameters in juvenile lobsters; ANOVA-analysis of variance

							Dorsal muscle		Shell, meat sail, chelae		Hepatopancreas			Calcium
Treatment	Expt. no.	Wt. (g)	Days on Expt.	No. molts	Molt stage	Serum Protein (mg/ml)	% Dry wt	% Protein dry wt	% Dry wt	% Lipid dry wt	% dry wt	% Lipid dry wt	% Glycogen	Shell (g/100g) dry wt
Ablation	1	25.2	174	8	D_2	37.5	23.0	81.5	34.5	1.69	30.3	36.7	1.17	—
"	1	20.2	174	7	D_2	43.5	23.9	84.3	30.9	—	32.6	37.4	1.43	24.9
"	1	22.1	174	8	D_2	22.0	20.0	81.6	35.5	2.64	27.3	22.0	1.07	27.7
"	2	11.5	96	4	D_1	14.8	18.9	76.0	27.7	3.08	28.5	44.6	—	30.3
"	2	9.4	96	4	D_1	19.7	19.9	74.4	28.8	1.31	25.6	28.9	0.56	—
"	2	7.2	96	3	D_0	21.5	20.0	—	31.0	1.87	33.4	46.3	1.11	30.7
"	2	7.5	96	4	D_1	24.5	21.8	76.6	30.4	2.25	33.4	44.7	0.94	25.7
"	2	11.2	96	4	D_0	15.5	19.6	73.9	29.4	1.40	30.4	37.5	1.12	22.5
Mean						24.9	20.9	78.3	31.0	2.03	30.2	37.3	1.06	27.0
±3 SE						8.4	1.5	3.6	2.2	1.59	3.4	6.9	0.24	3.2
Control	1	7.0	174	7	D_2	61.5	24.6	77.5	38.6	1.93	41.2	55.0	1.39	25.6
"	1	5.0	174	5	D_2	72.0	25.2	75.8	38.2	2.08	40.2	60.2	1.17	37.9
"	1	6.8	174	7	D_2	71.0	25.1	81.0	38.1	1.89	38.6	55.2	1.16	30.7
"	2	3.8	96	2	D_3	—	24.4	73.2	35.4	3.17	47.8	61.1	1.67	27.4
"	2	4.6	96	3	D_3	—	23.2	81.5	32.8	3.47	46.2	72.5	2.03	29.0
"	2	3.6	96	2	D_2	34.4	23.3	79.4	35.4	5.23	48.7	64.4	0.87	26.4
"	2	3.3	96	2	C	21.5	20.0	—	26.3	3.84	24.8	25.4	—	22.6
"	2	2.1	96	1	C	18.0	20.2	78.9	28.0	5.63	24.0	—	3.26	25.6
Mean						46.4	23.3	78.2	34.1	3.40	38.9	56.3	1.65	28.2
±3 SE						24.7	1.7	2.6	3.9	1.2	7.9	13.2	.72	3.8
ANOVA *P*						0.4	.10	.61	.12	.03	.02	.007	.16	.24

TABLE 5. Effect of diet on growth of eyestalk-ablated and control juvenile lobsters.

Group	No. lobsters	Mean % gain	Total no. molts	No. deaths	Mean intermolt period
		Diet 1 High Protein			
Ablated	4	70.4±9.3	8	2	28.8±3.8
Control	3	51.6±6.9	4	0	44.0±5.0
		Diet 2 Low Protein			
Ablated	4	51.0±7.9	8	2	32.0±3.0
Control	5	55.3±5.9	10	0	41.2±8.4
		FBS			
Ablated	4	78.7±12.0	6	0	28.0±5.0
Control	3	52.1±5.6	5	0	34.0±10.0

reported that the crayfish were only fed lightly. He found that there was a marked effect upon survival of eyestalkless crayfish when they were "fed as much as they could eat." Of the 44 ablated crayfish, 22 survived a second molt and 3 survived a third. Again the composition of the diet was not mentioned. The fact that diet played a significant role in survival of eyestalk-ablated crustaceans was, however, clear. Abramowitz and Abramowitz (1940) reported similar high mortalities associated with molting in the crabs (*Uca pugilators*) with eyestalks removed. These animals were fed a small piece of clam daily. Drach (1944) fed eyestalk-ablated prawns (*Leander serratus*) every day on an excess of spider crab (*Maia squinado*), and although the ablated animals had higher mortalities than controls, many animals survived to molt 3 times. The present report confirms the theory of Smith (1940) that diet plays a significant role in the survival of eyestalk-ablated lobsters.

Juvenile lobsters fed frozen brine shrimp for 4 mo, followed by formulated diets containing species normally included in the diet of wild lobsters (Weiss 1971), have successfully molted 9 times after eyestalk ablation and several are still surviving. In fact, three of the ablated lobsters in Experiment 1 successfully completed a 10th molt after the termination date, July 30. In Experiment 2, 100% of the ablated juveniles survived 96 days to termination of the experiment, molting 3 or 4 times. In his unsuccessful attempts to induce "precocious" molting in American lobsters (*H. americanus*), Flint (1972) fed his animals weekly on liver chunks. Rao et al. (1973) succeeded in inducing precocious molting in 4th stage juvenile lobsters fed "guppy food." However, none of these animals survived beyond

three molts. Sochasky et al. (1973) who induced molting in small sexually mature male and immature female lobsters did not mention what their animals were fed. Their high mortality suggests that their diet may also have been inadequate.

Other factors besides diet may have affected survival in previous studies on ablation. Carlisle and Butler (1956) and Passano (1960) have shown using other crustaceans that eyestalk ablation accelerates ovary development, and it is possible that sexual development has complicated the initial attempts to accelerate lobster molting. Sochasky et al. (1973) used immature female and small mature male lobsters in their successful eyestalk-ablation experiments. Rao et al. (1973) used 4th stage juveniles. Atema and Engstrom (1971) report that sexually mature females were used, but they give no data on mortality, accelerated rate of molt, or number of successful molts. Effect of sexual maturation and reproduction on survival of ablated lobsters is yet to be clarified.

The number of large or adult lobsters ablated in this study was not large enough to be of great statistical significance. Results do, however, show that lobsters large enough to be sexually mature can survive eyestalk ablation. Thus, the negative results of Flint (1972) were apparently not caused by the fact that he was working with adult lobsters. A question yet to be answered is whether or not eyestalk ablation will accelerate ovary development in lobsters as in other crustaceans (Carlisle and Butler 1956).

Although results reported here are of a preliminary nature, eyestalk-ablated lobsters can survive for extended periods of time. Because of the small numbers of animals and deficiencies in the experimental design, the survival results may not be truly representative. The only mortalities in the present study that appeared to be related to eyestalk ablation were the two in Experiment 1 and one in Experiment 3 that died within a day or two after the operation, and one death in the course of Experiment 1 that could not be attributed to some accident.

Addressing himself to the effect of ablation on weight gain in crabs (*E. sinensis*) at molt, Koch (1952) reported that the increases were simply the result of absorption of excess water. He measured total nitrogen in control and ablated crabs before and after molting and found that although the ablated crabs showed a greater increase in size after molting there was no increase in total nitrogen. He suggested that eyestalk ablation results in increased volume but no real growth process or tissue synthesis. Though greater weight gains occur in ablated lobsters at molt, results of the present study show that the real growth occurs during the intermolt period when new tissue is being synthesized. After 95 or 174 days of accelerated weight gains, ablated lobsters did have percent dry material and protein content equal to that of control lobsters. The only significant difference in composition was the slightly lower level of lipid deposition in muscle and hepatopancreas of ablated lobsters. This indicates an accelerated rate of protein deposition and tissue synthesis in the ablated animals.

In addition to accelerated growth rate, eyestalk ablation was noted to have several other effects on lobsters. Like the crayfish (Smith 1940) and the crab (Abramowitz and Abramowitz 1940) ablated juvenile lobsters became much paler in color after one or two molts. Colors ranged from pale orange to pale blue compared to the normal dark brown–green of controls. Sochasky et al. (1973) reported that ablated lobsters, though showing an accelerated molt rate, did not appear able to regenerate lost limbs and did not produce limb buds prior to molting. On the contrary, all ablated lobsters in the present study showed no difficulty in regenerating new limbs. Limb buds were produced after loss of a leg, chelae, or antennae prior to ecdysis. The absence of limb buds in the lobsters of Sochasky et al. might occur only in the first molt period after ablation or may be related to nutritional deficiencies.

Ablated lobsters also exhibited a new behavior not noted among controls. Often they would spend days on their backs with legs up, as though they had lost their balance and were unable to right themselves. This condition was reversible and did not seem to affect molting or growth. Ablated lobsters seemed to be much less active and/or agressive. They did not respond to lights being turned on or shadows of people passing in front of aquaria as did the controls.

Whether eyestalk ablation results in improved feed conversions or not, it does seem to have potential for application in commercial lobster culture. After 200 days ablated lobsters were 5 times as large as control animals. This increased growth rate would be invaluable to a lobster farmer. Eyestalk ablation might also have an important application in the present lobster fishery industry. Many lobsters are caught during the open season and held in large pounds until supplies are limited and price is high (McLeese and Wilder 1964). Due to deaths and cannibalism there is usually a net loss of weight in these pounds. Eyestalk ablation might lead to substantial gains in weight of lobsters and offset the normal shrinkage. There is still much research to be done on the effects of eyestalk ablation.

Though the protein content of the ablated animals is not different from the controls, the lower lipid content or some other factor will possibly result in an unacceptable flavor or texture of lobster meat. Though it is clear that diet plays a significant role in survival, little is known of the nutritional requirements of either ablated or control lobsters.

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Contribution of Gut Contents to the Concentration and Body Burden of Elements in *Tipula* spp. from a Spring-Fed Stream[1]

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ELWOOD, J. W., S. G. HILDEBRAND, AND J. J. BEAUCHAMP. 1976. Contribution of gut contents to the concentration and body burden of elements in *Tipula* spp. from a spring-fed stream. J. Fish. Res. Board Can. 33: 1930–1938.

Larvae of *Tipula* spp., a detritus-feeding aquatic insect collected from an unpolluted spring-fed stream, were analyzed for 30 elements before and after gut evacuation to determine the contribution of gut contents to whole-body concentrations. Chromium and Al concentrations were inversely related to body size, suggesting surface contamination. All elements analyzed except Na, Cr, Hg, Zn, and Se were significantly lower ($P < 0.01$) in concentration after gut evacuation (18% decrease for K to approximately 70% for V, Mn, Hf, and some of the rare earths). Ratios of variances of mean concentrations in organisms with guts filled to those with guts evacuated indicate that gut contamination is a major source of variation in measured whole-body concentrations of many elements. Calculated percentage of element body burden associated with gut contents ranged from <1% for Na to 89% for Zr, with a mean for all elements analyzed of 57 ± 8% (± 2 SE). Calculated trophic transfer factors (TTF = element concentration in larvae with guts evacuated/concentration in leaf detritus) for elements which are obtained primarily through the food chain were significantly >1 only for Zn; TTFs for all other elements were ≲ 1.

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Nous avons dosé 30 éléments avant et après évaculation du tractus digestif chez des larves de *Tipula* spp., un insecte détritivore recueilli dans un cours d'eau non pollué alimenté par des sources, dans le but de déterminer la contribution du contenu stomacal aux concentrations dans tout le corps. Les concentrations de Cr et d'Al sont en relation inverse de la grosseur du corps, ce qui suggère une contamination par la surface. Tous les éléments analysés, à l'exception du Na, Cr, Hg, Zn et Se, sont présents en concentrations significativement plus faibles ($P > 0.01$) après évacuation du tractus digestif (diminution variant de 18% pour le K à environ 70% pour le V, le Mn, l'Hf et quelques-unes des terres rares). Les rapports de variance des concentrations moyennes chez les organismes à tractus digestif plein à ceux d'organismes dont le tractus digestif est vide indiquent que la contamination par le tractus digestif est une source majeure de variation dans la mesure des concentrations de plusieurs éléments dans tout le corps. Le pourcentage calculé de la charge d'éléments dans le corps associée au contenu du tractus digestif varie de 1% pour le Na à 89% pour le Zr, la moyenne de tous les éléments analysés étant de 57 ± 8% (écart type ± 2). Les facteurs de transfert trophique calculés (FTT = concentration des éléments dans les larves avec tractus vide/concentration des détritus de feuilles) pour les éléments provenant surtout de la chaîne alimentaire ne sont significativement > 1 que pour le Zn; les FTT pour tous les autres éléments sont ≲ 1.

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ELEMENT concentrations in aquatic consumers are usually based on whole-body analysis, including the contents of the gastrointestinal (GI) tract (Lucas et al. 1970; Copeland and Ayers 1972; Mathis and Cummings 1973). The question arises as to whether the whole-body content of elements in aquatic species most accurately reflects tissue concentrations, or concentrations in gut contents and/or surface contaminants. Correction for these natural sources of contamination depends in part on whether one is interested only in the total element transfer between trophic levels or in both trophic level transfer and biological accumulation of elements within and between trophic levels. In both cases, however, the con-

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tribution to whole-body content of elements associated with surface and/or gut contaminants and the availability of these elements for absorption are necessary to determine biological concentration factors for trace contaminants released to the environment.

Organic and inorganic sediments and detritus are enriched in many elements relative to concentrations in organisms (Copeland and Ayers 1972; Bryan 1974), and inclusion of these materials either in the gut and/or on the body surface can produce significant errors in calculating whole-body tissue concentrations. The purpose of this study was to quantify the effects of gut contamination on whole-body concentrations of 30 elements in detritivorous *Tipula* spp. larvae and to determine the relationship between element concentrations in the larvae with those in their feces and food supply.

Materials and Methods

To estimate the magnitude of errors associated with including gut contents in *Tipula* spp. larvae, we measured whole-body concentrations of 30 elements in larvae before and after the larvae had egested their gut contents. Many *Tipula* spp. larvae are detritivores and typically are found in leaf packs in forested streams (Cummins 1973; Cummins et al. 1973). Our specimens were collected from a small, forested, spring-fed stream near the Oak Ridge National Laboratory in eastern Tennessee. Water quality is similar to that of other spring streams in the area that arise in dolomitic limestone (Elwood and Henderson 1975; Andren et al. 1975). *Tipula* spp. larvae were removed from leaf packs and carefully rinsed in stream water to remove surface contaminants. Approximately 150 larvae were placed in glass vials that had been washed with 6 N HNO_3. Larvae were then frozen immediately in dry ice. Samples of leaf detritus from the stream also were washed in stream water, placed in plastic bags, and frozen immediately in dry ice.

An additional 140 *Tipula* larvae were returned alive to the laboratory where they were allowed to egest the contents of their GI tract over a 3-day period. Larvae were placed in two plastic trays (70 larvae per tray) containing water from the stream in which they were collected and maintained at ambient stream temperature of 10.5 C. Feces were collected twice daily from each tray by transferring the larvae to fresh stream water and filtering the feces onto tared Nucleopore filters with a 0.4-μm pore size.

After the 3 days allowed for gut evacuation, larvae were rinsed in spring water, placed in glass vials, and frozen immediately in dry ice. *Tipula* and detritus samples were freeze-dried to a constant weight and subsamples were removed for chemical analyses. Feces samples were dried in a desiccator.

All samples were analyzed for element content using nondestructive neutron activation analysis (NAA). Impurities in the Nucleopore filters were determined by NAA and corrected for in feces samples. Analytical precision for NAA ranged from 1 to 30%, depending on the specific element.

Results and Discussion

Concentration and Body Size

Linear regressions of concentration of each element on mean dry weight per individual were calculated both for larvae with GI tracts filled (= initial concentration) and evacuated (= final concentration) to determine if there was a significant relationship between organism size and concentration. From the regression analyses the following observations were made: 1) For larvae with GI tracts filled, there was a highly significant inverse relationship (estimated slope was significantly < 0 for $P < 0.01$) between Cr concentration and mean individual dry weight (Fig. 1). For larvae with GI tracts filled, slopes of the remaining elements were not significantly different from zero ($P < 0.05$). 2) For larvae with GI tracts evacuated, there was a highly significant inverse relationship (estimated slope < 0 for $P < 0.01$) between concentrations of Cr and Al and mean dry weight (Fig. 1 and 2). All other slopes were not significantly different from zero ($P < 0.05$).

The reason for the inverse relationship between Cr and Al concentrations and size is not known, but probably is due either to surface contamination or absorption of Cr in solution by the integument of *Tipula* larvae. Copper in the polychaete, *Nereis diversicolor*, collected from con-

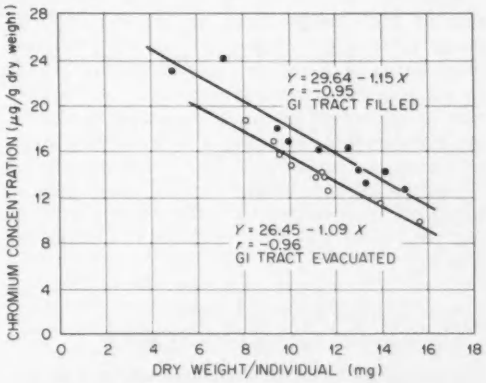

FIG. 1. Chromium concentration vs. mean individual dry weight of *Tipula* spp. larvae with GI tracts filled and evacuated. The two lines are significantly different ($P < 0.05$).

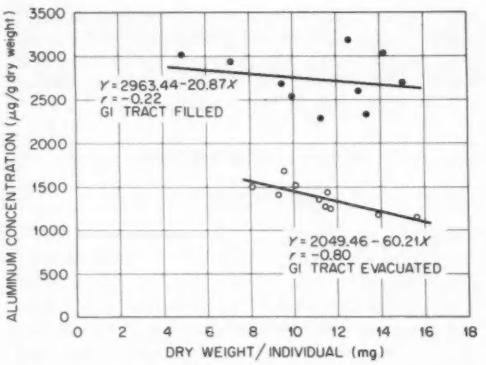

FIG. 2. Aluminum concentration vs. mean individual dry weight of *Tipula* spp. larvae with GI tracts filled and evacuated. The slope for organisms with GI tracts filled is not statistically significant ($P < 0.05$) but the slope for organisms with GI tracts evacuated is significant ($P < 0.01$).

taminated sediments in an estuary was shown to be concentrated (by chelation) in the epidermis (Bryan 1974). If chelation of certain metals by epidermal tissues of aquatic species such as *Tipula* occurs, this would explain the inverse relationship for Cr because smaller organisms have larger surface to volume (and mass) ratios. The fact that the slope for Al was not significantly different from zero for organisms with GI tracts filled (Fig. 2) is probably the result of masking of surface contamination by high concentrations of Al in the gut contents. Although all specimens were carefully washed prior to freezing for chemical analysis, clay particles with high Al concentrations could have adhered to the body surface.

Slopes of the two regressions of Cr concentration on body weight were not significantly different ($P < 0.05$) (Fig. 1). Since the difference in elevation of these two linear regressions is due to gut contamination, this suggests that the percent of dry weight of the animals associated with gut contents remains constant over the size range of *Tipula* larvae analyzed. The actual percentage of individual dry weight due to gut contents, based on fecal output over the 3-day period in the two pans, was 22.1 ± 1.7% ($\bar{X}$ ± 2 SE, $n = 2$).

Initial and Final Whole-body Concentrations and Body Burdens

Changes in Cr and Al concentrations with gut evacuation (i.e. difference between the initial and final concentration) as a function of initial dry weight were calculated using the regression equations in Fig. 1 and 2 and assuming that the final dry weight per individual was 78% of the initial dry weight. The change in Cr concentration with gut evacuation was not significantly different from zero over the entire size range of individuals analyzed as reflected by the fact that the 95% confidence region of the regression line (Fig. 3) includes the line $Y = 0$ over the entire range of initial dry weights per individual. For Al there was a highly significant decrease ($P < 0.01$) in concentration as reflected by the fact that the 95% confidence region of the regression line lies above the line $Y = 0$ over the entire size range of larvae analyzed (Fig. 3). The slope of the relationship between change in Al concentration with gut evacuation and initial dry weight per individual, however, was not significantly different from zero ($P < 0.05$).

For all other elements analyzed, comparisons of initial and final whole-body concentrations are based on mean concentrations in each analysis (Table 1). Differences between initial and final concentrations were tested using either a two-sample *t*-test or a modified *t*-test if variances of analysis means were significantly different from each other (Steel and Torrie 1960). For

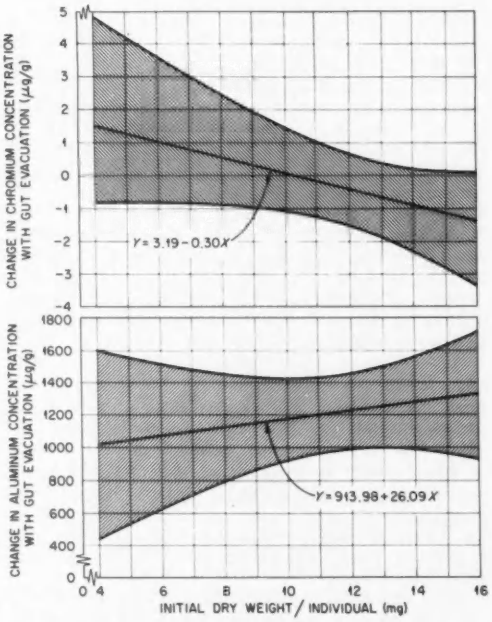
CHANGE IN CHROMIUM CONCENTRATION WITH GUT EVACUATION (μg/g)
Y = 3.19 - 0.30X
CHANGE IN ALUMINUM CONCENTRATION WITH GUT EVACUATION (μg/g)
Y = 913.98 + 26.09X
INITIAL DRY WEIGHT/INDIVIDUAL (mg)

FIG. 3. Calculated change in concentration of Cr and Al in *Tipula* spp. larvae with gut evacuation (i.e. initial–final concentration) as a function of initial dry weight per individual. Shaded area is the 95% confidence region.

TABLE 1. Mean whole-body concentration (±2 SE) of elements in *Tipula* sp. larvae before (initial) and after (final) gut evacuation, percent change in concentration, and the ratio of variances (s^2) of the initial to the final concentration. Values in parentheses are number of values from which mean concentrations were calculated.

Element	Concn (μg/g, *dry wt*)		% Change	$\left[\frac{s^2(\text{initial})}{s^2(\text{final})}\right]$
	Initial[a]	Final[b]		
Na	14730±874(10)	14989±911(10)	+1.8[c]	0.2
K	17720±841(10)	14540±785(10)	−18.0[d]	1.1
Rb	5.73±0.53(10)	3.01±0.51(7)	−47.5[d]	1.5
Cs	0.24±0.02(10)	0.13±0.02(10)	−45.8[d]	1.0
Ca	7070±2245(5)	2446±402(10)	−64.5[c,d]	15.6
Ba	55.1±7.3(10)	17.4±2.8(8)	−68.4[c,d]	8.8
Zr	26.1±4.6(6)	<20.0	—	—
Hf	0.32±0.06(10)	0.09±0.03(9)	−71.9[c,d]	6.2
Th	0.45±0.04(10)	0.22±0.02(10)	−51.1[d]	4.0
V	9.1±1.1(10)	2.5±0.3(10)	−72.1[c,d]	18.1
Ta	0.029±0.004(5)	<0.020	—	—
Cr	13.1±1.0[e](2)	14.2±0.5[e](2)	+8.9	3.1
Mn	658±68(10)	196±9(10)	−70.2[c,d]	59.5
Fe	2132±177(10)	1088±92(9)	−49.0[d]	4.1
Co	4.12±0.28(10)	2.93±0.17(9)	−28.9[d]	2.9
Zn	90.1±6.6(10)	106.4±4.7(9)	+18.0[d]	2.1
Hg	0.17±0.05(9)	0.22±0.06(10)	+29.4[c]	0.5
Al	2732±195(10)	1822±9[e](2)	−33.3[d]	3.4
Se	1.02±0.13(10)	0.95±0.11(10)	−6.9[c]	1.4
Cl	3442±183(10)	1774±262(10)	−48.5[d]	0.5
Br	60.8±7.7(10)	34.3±2.2(10)	−43.6[c,d]	12.2
I	8.83±1.72(4)	4.10±0.60(8)	−53.6[d]	4.1
Sc	0.80±0.12(10)	0.35±0.02(10)	−56.2[c,d]	22.6
La	5.32±1.40(8)	2.11±0.10(2)	−60.3[c,d]	800.0
Ce	4.71±0.37(10)	1.77±0.17(10)	−62.4[d]	4.6
Nd	5.27±2.15(7)	<5.01	—	—
Eu	0.118±0.025(10)	0.033±0.003(10)	−72.0[c,d]	64.0
Tb	0.093±0.024(10)	<0.026	—	—
Yb	0.31±0.06(10)	0.093±0.011(8)	−70.0[c,d]	44.4
Lu	0.108±0.023(10)	<0.097	—	—

[a] To convert concentrations to ash-weight basis, divide by 0.1494.
[b] To convert concentrations to ash-weight basis, divide by 0.1087.
[c] Modified two-sample *t*-test (Steel and Torrie 1960).
[d] Significant ($P < 0.01$).
[e] Values calculated using significant regression equations in Figs. 1 and 2 and mean individual initial and final weights in two replicates.

comparison with other elements, the decrease in concentration of Cr and Al was calculated from the regression equations in Fig. 1 and 2, utilizing the average initial and final dry weight (i.e. corrected for feces losses) per individual. Because final concentrations of Zr, Tb, Nd, Lu, and Ta were below detection limits, mean concentrations of these elements were not tested (Table 1). Except for Na, Cr, Se, Hg, and Zn, final concentrations were significantly lower ($P < 0.01$) for all of the remaining elements analyzed (Table 1), with the percentage decrease in concentration ranging from 18% for K to approximately 70% for V, Hf, and some of the rare earths. Final concentrations of Zn were significantly greater ($P < 0.01$), while Na, Cr, Se, and Hg were not significantly different ($P < 0.10$).

Table 1 shows that gut contents are a major contributor to whole-body concentrations of most elements. The fact that ratios of variances of the mean initial concentration to the mean final concentration are significantly > 1 for 12 of the elements analyzed (Table 1, last column) indicates that gut contamination also is an important source of variation in measured concentrations of several elements, particularly Ca, Sc, V, Mn, Br, and some of the rare earths. This is probably due to variation in the amounts of contamination from detritus and inorganic stream sediments in the GI tract.

TABLE 2. Weighted mean element concentrations in feces collected over the 3-day period of gut evacuation from *Tipula* spp. larvae, and percent of whole-body burden associated with gut contents. Except where indicated, initial body burden and gut burden are based on samples from the same set of organisms.

Element	Feces concn[a] ($\mu g/g$ *dry wt* $\pm$ 2 SE, $n = 2$)	% Body burden associated with gut contents ($\pm$2 SE)
Na	159.2±4.3	0.30±0.02
K	4855±4500	8.5±10.9
Rb	9.0±1.0	45.8±7.7
Cs	0.69±0.04	60.3±1.9
Ca	31700±1200	78.6±4.9
Ba	176.6±5.1	74.3±1.9
Zr	105.8±25.7	89.1±25.0[b]
Hf	1.60±0.13	83.3±4.2
Th	1.59±0.50	66.8±10.6
V	19.69±0.18	68.7±4.5
Ta	0.107±0.023	81.2±18.1[b]
Cr	39.39±0.67	40.1±2.5[c]
Mn	1223±17	63.9±4.3
Fe	4641±402	54.8±3.3
Co	6.92±0.21	40.2±1.4
Zn	763.9±216.5	66.4±10.8
Hg	2.155±0.084	73.8±10.0
Al	7837±273	61.9±3.9[d]
Se	0.987±0.019	22.9±3.0
Cl	950±9	13.3±1.1
Br	143±3	54.3±1.8
I	9.9±1.1	40.3±0.6
Sc	1.82±0.11	60.0±3.9
La	9.86±0.33	56.4 ($n = 1$)
Ce	14.40±0.63	69.8±2.6
Nd	10.34±1.75	43.2±7.2[b]
Eu	0.268±0.040	69.3±4.7
Tb	0.180±0.001	73.4±9.1
Yb	0.627±0.112	65.4±7.0
Lu	0.267±0.012	72.5±0.3
		Mean = 56.5±8.2 (n = 30)

[a]To convert to ash-weight basis, divide values by .2301.

[b]Initial body burden calculated from mean initial concentrations in Table 1.

[c]Body burden based on calculated final concentration using regression equation for organisms with guts evacuated (Fig. 1).

[d]Body burden based on calculated final concentration using regression equation for organisms with guts evacuated (Fig. 2).

Higher concentrations of Zn and Hg after gut evacuation (Table 1) suggest either contamination of organisms during the 3-day period of gut evacuation or in sample preparation, or dilution of whole-body concentrations by gut contents (i.e. feces of lower concentration than the body). Dilution of whole-body concentrations by gut contents does not explain the higher final concentrations, however, because feces are enriched in both of these elements (Table 2) relative to final concentrations in the body.

Although the observed decrease in whole-body concentration of most elements following defecation is probably due to the loss of elements associated with gut contents, some of the decrease may be due to excretion from tissues in a soluble form. Contribution of excretion to observed decreases in concentration cannot be determined without data on the excretion rates of these elements by Tipula larvae. Soluble salts, such as K, Na, and chloride, which are important in maintaining osmotic balance in aquatic insects and which can be resorbed from feces and absorbed directly from water, have a rapid turnover rate in aquatic insects (Shaw and Stobbart 1963). Because these *Tipula* larvae were kept in

ambient stream water during the 3-day period of gut evacuation, it seems unlikely that decreases in K and chloride concentrations are due to excretion. Published data on biological half-lives of radioisotopes of certain elements in aquatic and terrestrial invertebrates (Reichle et al. 1970) suggest that at least part of the decrease in concentrations of Ca, Rb, La, Co, Cs, and I could have been due to excretion of these elements in a soluble form over the 3-day period.

While these results show that gut contamination is a major contributor to measured whole-body concentrations of most elements, the question arises as to whether the final concentrations are representative of contamination-free samples. The inverse relationship between final Cr and Al concentrations and individual weight (Fig. 1 and 2) suggests that there was surface contamination on samples with guts evacuated. Because both detritus (Table 3) and suspended sediments in spring-fed streams in this area (Andren et al. 1975; A. Andren unpublished data) are enriched in most of these elements relative to concentrations in *Tipula* larvae, even a small amount of surface and/or gut contamination can increase the concentration. Copeland and Ayers (1972) suggested using concentrations of rare earths (including Sc) that are low in biological material and relatively high in geological material as a measure of sediment contamination in aquatic organisms. These authors found that for Sc concentrations > 0.1 ppm (dry weight) in samples of benthic invertebrates, zooplankton, and phytoplankton from Lake Michigan, Sc was directly related to concentrations of Fe, Co, and other trace metals. For Sc concentration < 0.1 ppm, however, Fe and Co appeared to be independent. Copeland and Ayers hypothesized that for samples of organisms in which Sc exceeded 0.1 ppm, sufficient Fe and Co was contributed from sediment contamination to mask the real concentration of these elements in biological materials. Their data suggest that for concentrations > 0.1 ppm in aquatic organisms in Lake Michigan, Sc increases exponentially in relation to Fe and Co.

The lowest final Sc concentration in *Tipula* spp. larvae was 0.29 ppm, suggesting that some sediment was still in these organisms after 3 days of gut evacuation. In addition, initial and final concentrations of Fe, Co, and Al in *Tipula* larvae are related significantly ($P < 0.01$) to Sc content (Fig. 4). Except for Co on Sc, the initial and final concentration regressions were found to be significantly different ($P < 0.05$). The common regression for all three elements is included in Fig. 4. With the exception of final Fe and Al concentrations (Fig. 4), slopes of Co on Sc, initial Fe on Sc, and initial Al on Sc are significantly less than one ($P < 0.05$). Even though a proportional relationship between Sc and final Fe and Al concentrations cannot be rejected, these results tend to support Copeland and Ayers' (1972) observation for Lake Michigan that in aquatic biota with Sc concentrations > 0.10 ppm (dry wt), Sc increases exponentially in relation to Fe and Co. This suggests that in contaminated organisms, Sc is enriched relative to the other three metals. This enrichment probably is due to differences in the geochemistry of these elements which are associated with sediments in the GI tract and/or body surface of this species.

To estimate the relative contribution of gut contents in the mass transfer of elements to predators feeding on *Tipula* larvae, the percent-

TABLE 3. Mean concentration of elements in leaf detritus and calculated trophic transfer factors $\left(\text{TTF} = \frac{\text{final concentration in } \textit{Tipula} \text{ spp.}}{\text{concentration in leaf detritus}}\right)$ in *Tipula* spp. larvae relative to leaf detritus.

Element	Concn in detritus[a] ($\mu g/g$ *dry wt* $\pm$ 2 ^{d}E)	TTF
Na	42.8±15.7 (5)	350
K	1006±88 (5)	14
Rb	all <3.19	—
Cs	0.14±0.03 (3)	0.9
Ca	19000±1850 (3)	0.8
Ba	62.8±24.6 (4)	0.3
Sc	0.54±0.35 (5)	0.6
La	5.20±8.50 (5)	0.4
Zr	all <51.0	—
Hf	0.23±0.12 (5)	0.4
V	6.02±3.31 (5)	0.4
Ta	all <0.044	—
Cr	36.0±3.8 (5)	0.4
Mn	501±344 (5)	0.4
Fe	1261±291 (5)	0.9
Co	3.07±0.64 (5)	1.0
Zn	36.5±9.6 (5)	29.0
Hg	0.13±0.03 (3)	1.7
Se	0.49±0.15 (3)	1.9
Al	1564±509 (5)	0.9
Cl	110±30 (3)	16
Br	18.4±6.0 (5)	1.9
I	all <6.2	—
Ce	3.78±1.90 (5)	0.5
Nd	all <10.6	—
Eu	0.182±0.150 (5)	0.2
Tb	0.15±0.12 (4)	—
Yb	0.41±0.33 (5)	0.2
Lu	0.21±0.15 (3)	—
Th	0.25±0.09 (5)	0.9

[a]To convert concentrations to ash-weight basis, divide values by 0.0746. Value in parentheses is number of values from which mean concentrations were calculated.

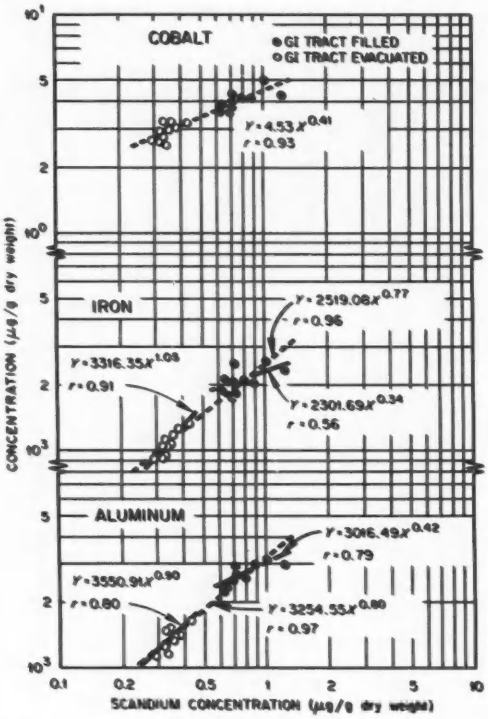

FIG. 4. Concentration of Sc vs. Al, Fe, and Co in *Tipula* spp. larvae with GI tracts filled and evacuated. Dashed line is the common regression for initial and final concentrations combined.

age of element body burden associated with gut contents was calculated by dividing the gut burden (amount of element per individual associated with gut contents collected over the 3-day period) by the initial whole-body burden. The initial whole-body burden was calculated as the sum of the gut burden, plus the product of the mean final concentration (Table 1) and the calculated mean final dry weight per individual. Initial body burdens of Cr and Al were based on an individual of the same initial dry weight, using final concentrations calculated from the regression equations in Fig. 1 and 2. Percentage of the initial body burden associated with gut contents ranged from $< 1\%$ for Na to 89% for Zr (Table 2). Average percentage of the body burden associated with gut contents for all 30 elements was $57 \pm 8\%$ (± 2 SE). Over 50% of the body burden was associated with gut contents in 70% of the 30 elements analyzed.

Differences between the percentage decrease in concentration with gut evacuation (Table 1) and the percent of the initial body burden associated with gut contents (Table 2) depend, in part, on the relationship between concentration in feces and *Tipula* larvae. For most elements, the feces (Table 2) are enriched relative to both final concentrations in *Tipula* (Table 1) and concentrations in leaf detritus (Table 3). This apparent enrichment of elements in feces is probably due in part to absorption of organic matter from the detritus by *Tipula* larvae as suggested by the fact that the average organic content of feces (based on dry weight loss on combustion at 450 C) was $77.0 \pm 2.0\%$ (± 2 SE, $n = 5$) while that in leaf detritus was $92.2 \pm 0.5\%$ ($n = 4$). It could also be due in part to selective feeding by *Tipula* on leaf detritus with element concentrations greater than those measured (Table 3).

Increased ingestion rates of, and feeding preference for, conditioned leaf detritus by stream detrivores have been demonstrated (Cummins 1974). The in-stream conditioning involves colonization by microflora (algae, bacteria, fungi) and successional changes in the biochemistry of the detritus, including increases in both the relative and absolute nitrogen (protein) content (Kaushik and Hynes 1971; Iversen 1973; Triska et al. 1975). Nitrogen enrichment in leaf detritus is the result of nitrogen fixation by the associated microflora. Successional enrichment in other elements, including Mn, Fe, Cu, Cd, and Hg, of decomposing mangrove detritus in Florida estuaries also has been observed (Mathis 1973; Linberg and Harriss 1974) suggesting that microflora associated with detritus in aquatic environments may be responsible for the enrichment of additional elements besides nitrogen.

Leaching of elements from feces would result in an underestimate of the percent of the element body burden associated with gut contents. Thus, detritus-feeding aquatic insects are known to enhance remineralization of some elements, including Ca, Mg, and K, in leaf detritus through feeding and egestion (Woodall 1972).

It is revealing to examine the distribution of the percentage of the 30 elements analyzed which exceeded a given percent of element body burden associated with gut contents (Fig. 5). As this figure shows, gut contamination is a potential problem for all of the 30 elements analyzed. Also, while based on less than 30% of the elements, this figure contains examples from most element groups in the periodic table and, thus, we contend that the general distribution of elements would probably not change significantly if the remaining elements were included. Further, if all sources of contamination were accounted for (i.e. surface and gut contamination), the distribution would be shifted to the right (i.e. for

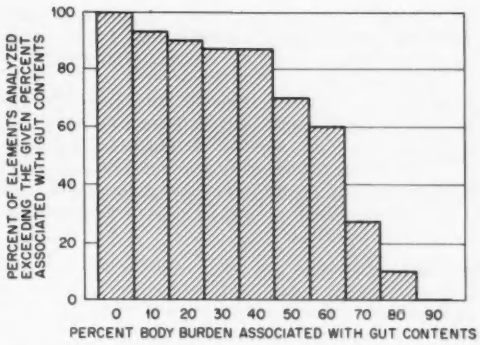

FIG. 5. Distribution of percent of the 30 elements analyzed which exceeds the given percent of body burden associated with gut contents in *Tipula* spp. larvae.

some percent of elements in the periodic table, more than 90% of the body burden in *Tipula* larvae would be associated with gut contents and surface contaminants).

TROPHIC TRANSFER OF ELEMENTS

To determine if there is food chain enrichment of the 30 elements analyzed, trophic-transfer factors (TTF), defined as the ratio of the concentration of elements (on a dry weight basis) in *Tipula* larvae with GI tract evacuated to concentration in leaf detritus (dry weight basis) were calculated (Table 3). Most of the calculated ratios are < 1, indicating that enrichment of most elements is not occurring at this level of the detritus food chain. The only elements with TTF > 1 are Na, K, Cl, Br, Zn, Hg, and Se. Values for Zn and Hg probably are in error, however, because of contamination of larvae as previously discussed. For elements that can be absorbed directly from water, such as Na, K, and Cl, the TTF is meaningless because the food chain is a minor pathway of accumulation. For elements with large distribution coefficients, K_d, (= element concentration in particulate materials on a weight basis to concentration in water), the TTF is a more meaningful value for comparing the relative bioaccumulation of elements because the food chain is the major pathway of accumulation for such elements by aquatic consumers. Possible reasons for the TTF < 1 are: there is discrimination against most of the elements analyzed; the elements are biologically unavailable to *Tipula* larvae from the detritus food source; or available amounts in detritus are masked by large unavailable amounts in contaminating stream sediments that are ingested.

While this study documents the contribution of gut contents to the whole-body concentrations of elements for only one detritus-feeding aquatic insect, it also raises questions about the accuracy of interpretation of published concentration factors and body burdens of elements in aquatic organisms where correction for or removal of surface and gut contaminants has not been done. In addition, these results demonstrate the potential importance of gut contents to the trophic transfer of elements in an aquatic food chain.

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Cadmium and Zinc Toxicity to flagfish, *Jordanella floridae*

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SPEHAR, R. L. 1976. Cadmium and zinc toxicity to flagfish, *Jordanella floridae*. J. Fish. Res. Board Can. 33: 1939–1945.

Cadmium and zinc toxicity to the flagfish (*Jordanella floridae*) was determined on the basis of 96-h median lethal concentrations (LC50) and significant decreases ($P = 0.05$) in survival, growth, and reproduction over the complete life cycle of the fish. The 96-h LC50 values for cadmium and zinc to juvenile flagfish were 2500 and 1500 μg/liter, respectively. In chronic tests, reproduction was the most sensitive indicator of cadmium toxicity and was inhibited at 8.1 μg/liter. Tissue-concentration analysis showed that fish exposed to concentrations of 1.7 μg/liter and above accumulated significantly greater amounts of cadmium than those in the controls. In zinc tests, survival of larvae (not exposed as embryos) and growth of females were the most sensitive measure of zinc toxicity and were reduced at respective concentrations of 85 and 51 μg/liter. Significant uptake of zinc occurred in fish exposed to concentrations of 47 μg/liter and above. The lowest cadmium and zinc concentrations causing adverse effects to the flagfish were similar to those affecting other fish species. Application factors for both metals were similar to those reported for cadmium exposed bluegills (*Lepomis macrochirus*) and zinc exposed fathead minnows (*Pimephales promelas*) in hard water.

SPEHAR, R. L. 1976. Cadmium and zinc toxicity to flagfish, *Jordanella floridae*. J. Fish. Res. Board Can. 33: 1939–1945.

Nous avons mesuré la toxicité du cadmium et du zinc chez *Jordanella floridae* en nous basant sur les concentrations létales médianes après 96 h (CL50) et sur des diminutions significatives ($P = 0.05$) de survie, de croissance et de reproduction durant un cycle biologique complet du poisson. Les CL50 après 96 h de cadmium et de zinc pour des *Jordanella* juvéniles sont de 2500 et 1500 μm/litre respectivement. Dans des essais chroniques, la reproduction est l'indicateur le plus sensible de toxicité du cadmium et est inhibée à 8.1 μg/litre. L'analyse des concentrations tissulaires démontre que les poissons exposés à des concentrations de 1.7 μg/litre et plus accumulent des quantités de cadmium nettement supérieures à celles des témoins. Dans des essais au zinc, la survie des larves (non exposées comme embryons) et la croissance des femelles sont les indicateurs les plus sensibles de toxicité du zinc et sont toutes deux réduites à des concentrations respectives de 85 et 51 μg/litre. Il y a assimilation significative de zinc chez les poissons exposés à des concentrations de 47 μg/litre et plus. Les concentrations minimums de cadmium et de zinc ayant des effets nocifs sur *Jordanella* sont semblables à celles qui affectent les autres espèces de poissons. Les facteurs d'application des deux métaux sont semblables à ceux qui ont été signalés pour des crapets arlequins (*Lepomis macrochirus*) exposés au cadmium et pour des têtes-de-boule (*Pimephales promelas*) exposés au zinc dans de l'eau dure.

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CADMIUM and zinc occur simultaneously in the environment (Lingane 1966; Schroeder et al. 1967) and are toxic to fish (National Academy of Sciences 1973). Although most toxicity tests with fish have been short-term acute exposures, an effort is being made at the Environmental Research Laboratory-Duluth to determine more sensitive effects of toxicants through chronic exposures of fish over their complete life cycle. Commonly used species, such as fathead minnows (*P. promelas*), bluegills (*L. macrochirus*), brook trout (*Salvelinus fontinalis*), and rainbow trout (*Salmo gairdneri*), however, require long testing periods (5 mo–3 yr) to obtain complete life cycle data. Smith (1973) has proposed the use of the flagfish (*Jordanella floridae*) for rapid chronic bioassays because of its short generation time (6–8 wk) and other unique features. Little information has been shown on the effects of toxicants on this species in the literature (Foster et al. 1966, 1969).

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The purpose of this work was to determine the toxicity of cadmium and zinc to the flagfish by studying the effects of these metals on all developmental stages of the life cycle. In addition, this study was designed to evaluate the application-factor concept (Mount and Stephan 1967b) with a species not previously tested.

Materials and Methods

Water Characteristics

Untreated Lake Superior water was used in all tests at 25 ± 2 C. Chemical characteristics of the test water were analyzed weekly according to methods described by the APHA et al. (1971). Means and ranges (in parentheses) for these measurements were (milligrams/liter): dissolved oxygen, 8.3 (7.2–9.5); hardness, 44 as $CaCO_3$ (41–46); alkalinity, 42 as $CaCO_3$ (39–44); and acidity, 2.4 as $CaCO_3$ (1.5–3.4). The pH ranged from 7.1 to 7.8.

Exposure System

The exposure system consisted of a proportional diluter (Mount and Brungs 1967) which delivered five toxicant concentrations and a control to duplicate exposure chambers. Spawning chambers were glass aquaria, 30 × 60 × 30 cm, with a water volume of 43 liters. Larval chambers were 15 × 53 × 22 cm and contained 22 liters of water. Flow rate to each spawning chamber was 15 liter/h providing 95% replacement of test water every 9 h (Sprague 1969).

Fluorescent bulbs provided a light intensity of 50 lm at the water surface. An automatically controlled 16-h photoperiod was used.

Toxicant Solution

Stock solutions were prepared by dissolving reagent-grade $CdCl_2$ and $ZnSO_4 \cdot 7H_2O$ in 15 liters of distilled water and were introduced from a Mariotte bottle to the diluter by a chemical metering device (McAllister et al. 1972). Weekly composite samples of the test water were analyzed by a Perkin Elmer Model 403 atomic absorption spectrophotometer. Measurements for cadmium concentrations in the water are included in Table 1 and those for two zinc tests are shown in Tables 2 and 3. Analysis of variance showed that zinc measurements were the same for the two tests. Calibration curves were constructed by adding known amounts of cadmium and zinc to Lake Superior (control) water. Mean percent recovery and standard deviation for 16 spiked cadmium and zinc samples were 91 ± 0.8 and 100 ± 2.0, respectively.

Tissue Analysis

Whole fish from each concentration were analyzed for cadmium and zinc after 30 days of exposure and at the end of the test (approximately 100 days). For the cadmium test, 10 fish were analyzed per concentration except at 16 and 31 μg/liter where only 1 and 4 fish survived, respectively. Five fish were analyzed per concentration in each of the two zinc tests. A 95–100% recovery of the metals for 35 spiked tissue samples was obtained using a wet digestion, atomic absorption spectrophotometric analysis (Leonard 1971).

Biological Procedures

In chronic tests, enough embryos were incubated in each exposure concentration (cadmium test, zinc test 1) or in the controls (zinc test 2) to provide 30 1-day-old larvae to each chamber for the start of the tests. Exposed larvae and larvae not previously exposed as embryos were utilized for zinc exposures to determine the effect of embryo acclimation on larval sensitivity. To control fungus, all embryos were treated with metal-free malachite green (4 mg/liter) for 10 min during the first 3 days of incubation.

Larvae were fed brine shrimp nauplii 4 times a day for the first 30 days. After this time, all fish were randomly reduced to 15 per chamber and fed a diet of frozen brine shrimp twice a day and salmon starter granules once a day. The number of fish per chamber was further reduced to two males and five females after males began displaying territorial behavior, about the 60th day of the test.

Reproduction studies were started after 30 or more embryos appeared on any one spawning substrate and were continued for a period of 45 days. Spawning substrates were approximately 13 × 8 cm and made from 20-mesh stainless steel screen that was corrugated and wrapped in dark orlon yarn. After spawning, 30–50 embryos were removed from the substrates, placed in oscillating egg cups (Mount 1968), and incubated in the test water. All embryos not incubated for hatchability determinations were counted and discarded.

Twenty newly hatched (F_1) larvae from each toxicant concentration were randomly selected and transferred to duplicate larval chambers for 30-day growth and survival exposure. In the cadmium test, control larvae were also transferred for 30 days to concentrations causing adverse effects to parental fish.

Flow-through 96-h acute toxicity tests were conducted in the chronic-test diluter system with juvenile flagfish 4–5 wk old, according to methods described by the APHA et al. (1971). The 96-h LC50 values were derived by graphical interpolation and used in the determination of application factors (maximum acceptable toxicant concentration [MATC]/96-h LC50) (Mount and Stephan 1967b) for both metals.

Statistical Analysis

For statistical evaluation, survival, growth, reproduction, and cadmium tissue-accumulation data were subjected to an analysis of variance ($P = 0.05$) and Dunnett's two-tailed comparison of treatment means to control means ($P = 0.05$) (Steel and Torrie 1960). A two-way analysis of variance was applied

TABLE 1. Survival, growth, and reproduction of flagfish (*Jordanella floridae*) exposed to several concentrations of cadmium; *$P = 0.05$ (significantly different from control according to Dunnett's procedure).

	Measured Cd concn (*µg/liter*)											
	31 ± 5.6[a]		16 ± 2.9		8.1 ± 2.0		4.1 ± 0.81		1.7 ± 0.52		0.11 ± 0.07 (control)	
	A[b]	B[b]	A	B	A	B	A	B	A	B	A	B
						30 days						
Survival (%)[c]	70	10	77	77	77	97	87	93	97	100	97	97
Mean total length (*mm*)	16 ± 1.5*	—	19 ± 1.6	18 ± 2.3	18 ± 0.7	20 ± 1.7	20 ± 1.9	18 ± 2.3	18 ± 3.5	17 ± 2.1	20 ± 1.0	19 ± 1.7
						100 days						
Males/females at termination	0/0	0/1	0/3	0/1	2/5	2/5	2/5	2/5	2/5	2/5	2/5	2/5
Mean total length (*mm*)												
Male	—		—		49 ± 7.8 (4)		53 ± 1.7 (4)		52 ± 1.7 (4)		55 ± 3.3 (4)	
Female	31 (1)[d]*		33 ± 2.1 (4)*		43 ± 3.2 (10)		43 ± 3.1 (10)		43 ± 2.2 (10)		45 ± 2.9 (10)	
Mean spawnings/female	0 *	0	1.7 *	1.0	5.2 *	3.0	10.4	8.6	11.0	11.4	8.8	8.4
Total embryos produced	0 *	0	163 *	35	1560 *	1270	3320	3280	4240	3440	3220	3430
Mean hatchability (%)	—		68		66		73		66		66	

[a]Mean ± SD.
[b]Duplicate chamber.
[c]Thirty fish per chamber.
[d]Number of fish analyzed.

TABLE 2. Survival, growth, and reproduction of flagfish (initially exposed as embryos) at several concentrations of zinc (test 1); *$P = 0.05$ (significantly different from control according to Dunnett's procedure).

	Measured Zn concn (*µg/liter*)											
	267 ± 28[a]		139 ± 18		75 ± 11		47 ± 11		28 ± 11		10 ± 13 (control)	
	A[b]	B[b]	A	B	A	B	A	B	A	B	A	B
						30 days						
Survival (%)[c]	10*	0	70	80	100	97	90	100	83	90	83	97
Mean total length (*mm*)	—	—	18 ± 2.2[a]	18 ± 0.9	18 ± 2.0	18 ± 1.4	19 ± 1.7	19 ± 1.8	18 ± 2.7	19 ± 2.0	18 ± 2.5	19 ± 2.0
						100 days						
Males/females at termination	0/0	0/0	0/4	2/5	2/5	2/5	2/5	2/5	2/5	2/5	2/5	2/5
Mean total length (*mm*)												
Male	—	—	45 ± 5.7 (2)[d]		51 ± 4.5 (4)		55 ± 2.7 (4)		56 ± 3.4 (4)		54 ± 3.4 (4)	
Female	—	—	40 ± 6.0 (9)		43 ± 2.5 (10)		43 ± 1.9 (10)		43 ± 2.4 (10)		43 ± 2.2 (10)	
Mean spawnings/female	—	—	0.3	1.4	4.0	4.6	9.4	3.4	4.8	4.4	10.8	4.8
Total embryos produced	—	—	130	197	1310	1650	3230	995	1560	1240	3650	1190
Mean hatchability (%)	—		73		59		72		76		70	

[a]Mean ± SD.
[b]Duplicate chamber.
[c]Thirty fish per chamber.
[d]Number of fish analyzed.

TABLE 3. Survival, growth, and reproduction of flagfish (not exposed as embryos) at several concentrations of zinc (test 2); *$P = 0.05$ (significantly different from control according to Dunnett's procedure).

	Measured Zn concn (*μg/liter*)											
	267 ± 28[a]		139 ± 18		85 ± 11		51 ± 9		26 ± 8		< 1.0 (control)	
	A[b]	B[b]	A	B	A	B	A	B	A	B	A	B
30 days												
Survival (%)[c]	0*	0	0*	0	20*	23	82	97	93	93	93	87
Mean total length (*mm*)	—	—	—	—	—	—	22 ± 2.3[a]	21 ± 3.5	21 ± 1.7	22 ± 1.8	23 ± 2.4	22 ± 2.4
100 days												
Males/females at termination	0/0	0/0	0/0	0/0	2/3	3/4	2/5	2/5	2/5	2/5	2/5	2/5
Mean total length (*mm*)												
Male	—	—	—	—	52 ± 8.4 (5)[d]		53 ± 2.9 (4)		53 ± 1.7 (4)		54 ± 1.8(4)	
Female	—	—	—	—	36 ± 4.6 (7)*		38 ± 5.5 (10)*		40 ± 3.5 (10)		43 ± 2.5 (10)	
Mean spawnings/female	—	—	—	—	4.0	0.3	2.2	6.6	5.4	3.2	9.4	4.6
Total embryos produced	—	—	—	—	322	11	272	2440	1050	348	2320	1360
Mean hatchability (%)	—		—		88		83		83		69	

[a]Mean ± SD.
[b]Duplicate chamber.
[c]Thirty fish per chamber.
[d]Number of fish analyzed.

to zinc-accumulation data for comparisons between tests.

Results

Cadmium Toxicity

In 30 days, the highest concentration (31 μg/liter) retarded growth and appeared to reduce survival (Table 1). Survival also appeared reduced at the next lower concentration (16 μg/liter). However, due to the variability of response in duplicate chambers, statistical significant differences ($P = 0.05$) in survival could not be shown in any of the concentrations. Additional mortality occurred at 16 and 31 μg/liter after this period and by the 60th day, survival was less than 35% and growth of fish at 16 μg/liter appeared to be reduced. Cadmium-induced mortalities of fish were always preceded by periods of involuntary muscle spasms. At the end of the test (approximately 100 days) all males were dead in the two highest concentrations and growth of five surviving females was significantly reduced. Mean spawnings per female and embryo production were adversely affected at 8.1 μg/liter (Table 1). No significant differences in survival, growth, or reproduction were observed below 8.1 μg/liter.

Embryos from exposed parents incubated at 16 μg/liter and below hatched as well as those in the control (Table 1). Survival and growth of F_1 larvae were not adversely affected at these concentrations after 30 days of exposure; however, survival of larvae transferred at hatch from control water to 31 μg/liter was less than 20%. No adverse effects were seen when control larvae were transferred to 16 μg/liter and below for this period.

The 96-h LC50 value calculated for 4–5-wk-old juveniles was 2500 μg Cd/liter.

Fish exposed for 30 days to concentrations of 1.7 μg Cd/liter and above contained significantly higher amounts of cadmium than did those in the controls (Fig. 1A). Cadmium uptake increased with increasing exposure concentrations but leveled off at 16 μg/liter. Concentrations of cadmium (micrograms per gram) were lower in fish exposed for 100 days than those exposed for 30 days, but older fish contained a significantly higher total body content (micrograms per fish). In addition, cadmium concentrations in 30-day-old exposed parental fish and progeny (F_1) were similar.

Zinc Toxicity

Test 1 — Survival of larvae previously exposed to zinc as embryos was reduced at 267 μg/liter after 30 days (Table 2). After 100 days of exposure, all fish had died at this concentration and growth of males was less than those of the controls at the next lower concentration (139 μg/liter). Mean spawnings per female and embryo production appeared to be reduced at 139 μg/liter but significant differences could not be shown due to the variable response.

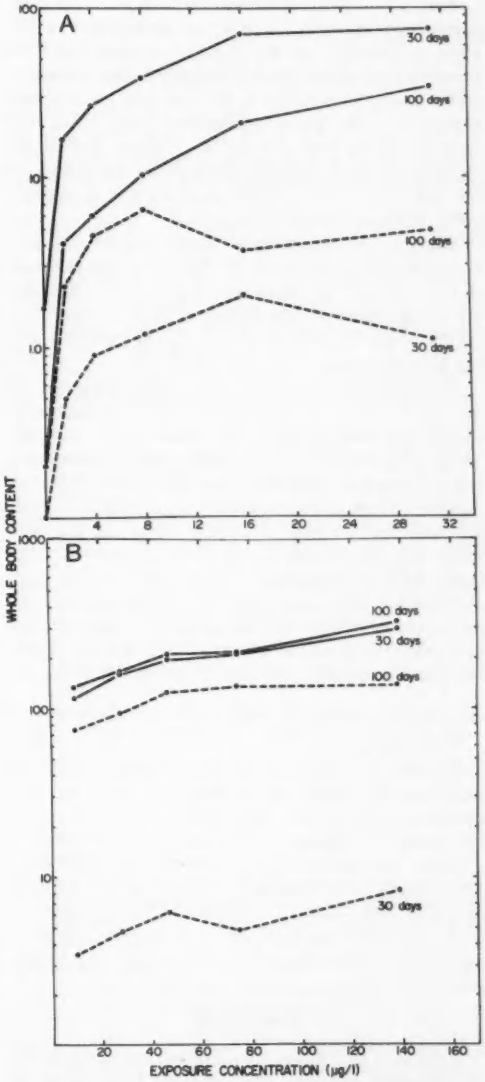

FIG. 1. Log cadmium (A) and zinc (B) content measured from whole body tissue of flagfish (*Jordanella floridae*) exposed to several cadmium concentrations for 30 and 100 days. Solid lines, micrograms per gram; dotted lines, micrograms per fish.

Test 2 — After 30 days, survival of larvae not previously exposed to zinc as embryos was adversely affected at 85 μg/liter (Table 3). No larvae survived at the two highest concentrations (139 and 267 μg/liter). By the end of the test, female growth was significantly lower than the controls at 85 and 51 μg/liter. Mean spawnings per female and embryo production appeared to be reduced at 85 μg/liter but were not statistically different from the controls.

Embryo hatchability (Tables 2 and 3) and survival and growth of F_1 larvae from exposed parents at 139 μg/liter and below were not significantly different from those of control larvae.

The 96-h LC50 value calculated for 4–5-wk-old juveniles was 1500 μg Zn/liter.

Fish exposed for 30 days to concentrations of 47 μg Zn/liter and above contained significantly higher amounts of zinc than those in the controls (Fig. 1B). Additionally, zinc uptake increased with increasing exposure concentrations. Concentrations of zinc (micrograms per gram) in fish exposed for 30 and 100 days were similar but older fish contained a significantly higher total body content (micrograms per fish). Zinc concentrations were also similar in 30-day-old exposed parental fish and progeny (F_1) and in fish previously exposed as embryos (test 1) and those not previously exposed (test 2) after 100 days.

Resulting Test Values and Application Factors

Results described above for chronic effects of cadmium and zinc on survival, growth, and reproduction establish the MATC (as described by Mount and Stephan 1967b) between 4.1 and 8.1 μg/liter cadmium and 26 and 51 μg/liter zinc. The application factor (MATC/96-h LC50) based on the 96-h LC50 values of 2500 μg Cd/liter and 1500 μg Zn/liter was between 0.0016 and 0.0032 for cadmium and 0.017 and 0.034 for zinc.

Discussion

Response of flagfish to sublethal concentrations of cadmium and zinc was different from those of other tested species. Pickering and Gast (1972) and Eaton (1974) found that embryos of fathead minnows and larvae of bluegills were the stages most sensitive to cadmium exposure. However, in the present study, spawning and embryo production were the most sensitive measures of effect. For zinc tests, survival of flagfish larvae and adult growth were adversely affected at lower concentrations than those affecting reproduction. This finding was different than the results of fathead minnow zinc exposures conducted by Brungs (1969). He found that reproduction was the most sensitive measure of zinc toxicity. Although the response of flagfish to cadmium and zinc was different from that of exposed fathead minnows and bluegills, the present results indicate that flagfish sensitivity was similar to that of cadmium-exposed brook trout (Benoit et al. 1976) and zinc-exposed rainbow trout (Sinley et al. 1974) tested in soft water.

In this test, larvae previously exposed to cadmium and zinc as embryos were more tolerant than those not previously exposed. This effect was much more pronounced in zinc tests as indicated by results shown in Tables 2 and 3. Sinley et al. (1974) reported that rainbow trout not exposed to zinc as embryos may be as much as 4 times more susceptible to zinc than fish previously exposed as embryos. Although the mechanism for this phenomenon is poorly understood, Wedemeyer (1968) showed that coho salmon (*Oncorhynchus kisutch*) eggs accumulate zinc highest in the chorion (70%), but that the developing embryos accumulate only a small amount (1%). Wedemeyer also pointed out that malachite green concentrations greater than 5 ppm increased zinc permeability of the vitelline membrane, thereby increasing the uptake of zinc in the yolk. Although the malachite green concentrations used to control fungal growth in the present tests were lower than those increasing zinc permeability, the danger exists that the toxicity of zinc was affected to some extent. No attempt was made to study the effects of this dye on zinc uptake in this test. The known action of malachite green on zinc and possibly other pollutants suggests, however, that it should not be used in toxicity studies.

Relationships between cadmium tissue uptake and water concentration in this test were similar to those observed by Mount and Stephan (1967a) for cadmium-exposed bluegills. The leveling-off of cadmium uptake at 16 μg/liter indicates that a possible equilibrium was reached between cadmium concentrations in the water and in the tissues. Comparisons between 30- and 100-day-exposed fish and accumulations expressed on a concentration (micrograms per gram) and total uptake (micrograms per fish) basis (Fig. 1A) show that cadmium accumulated with age, but at a rate that was slower than the growth of the fish. Similar results were indicated for the uptake of zinc (Figure 1B). Absence of significant additional metal uptake on a concentration basis was probably related to mechanisms affecting rates of uptake and elimination as was proposed by Coleman and Cearley (1974) for silver uptake in largemouth bass (*Micropterus salmoides*) and bluegills. Additionally, tissue concentration did not differ significantly between fish

exposed to zinc as embryos and those not previously exposed. This was attributed to the inability of zinc to penetrate the egg chorion to a large extent as was discussed by Wedemeyer (1968). Similar tissue concentrations in parents and progeny were probably the result of the same phenomenon. Experiments involving embryo and larval analyses would help to clarify mechanisms of metal uptake.

Abnormal behavior of exposed fish occurred at cadmium and zinc concentrations that caused death and inhibited reproduction. Cadmium especially had this effect on male fish during spawning. Eaton (1974) and Benoit et al. (1976) saw similar behavior in cadmium-exposed bluegills and brook trout. Abnormal behavior of bass and bluegills (uncontrolled swimming movements, convulsions, loss of equilibrium, and apparent coma) was also observed by Cearley (1971) when these fish were exposed to cadmium and silver. This type of behavior was attributed to the inhibition of acetylcholinesterase, causing death by paralysis of the muscles of respiration and/or depression of the respiratory center.

Flagfish application factors reported here for cadmium and zinc were similar to those reported by Eaton (1974) and Brungs (1969) for cadmium-exposed bluegills and zinc-exposed fathead minnows, respectively. Since bluegill and fathead minnow tests were conducted in hard water compared to the soft water of this test, water hardness, at least for these tests, would apparently not affect the estimation of chronic safe concentrations for these metals on the basis of calculated application factors.

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Influence of Food Competition, Predation, and Cannibalism on Walleye (*Stizostedion vitreum vitreum*) and Sauger (*S. canadense*) Populations in Lake of the Woods, Minnesota[1]

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SWENSON, W. A., AND L. L. SMITH JR. 1976. Influence of food competition, predation, and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota. J. Fish. Res. Board Can. 33: 1946–1954.

Feeding relationships between walleye, *Stizostedion vitreum vitreum*, and sauger, *Stizostedion canadense*, in Lake of the Woods, Minnesota, were investigated. Effectiveness of food consumption estimates in measuring feeding interactions was defined. Differences in walleye and sauger distribution, food habits, and feeding strata reduced interactions. Walleye feeding rate varied from 0.5 to 4.1% of body weight per day and was limited by prey abundance during June and July. Higher August and September prey densities did not influence walleye food consumption. Daily food consumption of sauger varied from 0.5 to 3.5% of body weight independent of changes in food availability. Relationships between the number of prey consumed daily by walleye and sauger and the decline in abundance of prey species suggested that predation was important in controlling food availability, and was the major cause of food competition and its limiting effect on walleye growth.

Analysis of commercial catch statistics suggested that factors other than predation influenced walleye survival. However, the relationship between the number of young-of-the-year walleye consumed and their abundance in the lake demonstrated predation by sauger may be important to walleye survival.

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Les auteurs étudient les relations alimentaires entre le doré jaune, *Stizostedion vitreum vitreum*, et le doré noir, *S. canadense*, dans le lac des Bois, Minnesota. Ils définissent l'efficacité des estimés de consommation d'aliments dans la détermination des interactions alimentaires. Des différences dans la répartition, les habitudes alimentaires et les paliers d'alimentation entre les deux espèces diminuent les interactions. Le taux d'alimentation du doré jaune varie de 0.5 à 4.1% du poids corporel par jour et est limité par l'abondance des proies en juin et juillet. Une plus grande densité de proies en août et septembre n'affecte pas la consommation d'aliments par le doré jaune. La consommation quotidienne d'aliments par le doré noir varie de 0.5 à 3.5% du poids corporel, indépendamment des variations dans la disponibilité de la nourriture. La relation entre le nombre de proies consommées quotidiennement par le doré jaune et le doré noir, et le déclin d'abondance des espèces proies donne à croire que la prédation est un facteur important de contrôle de la disponibilité de la nourriture et est la cause majeure de la compétition alimentaire et de ses effets sur la croissance du doré jaune.

L'analyse des statistiques de prises commerciales n'indique pas que la prédation limite la survie du doré jaune, mais suggère que d'autres facteurs non identifiés influent sur la survie. La relation entre le nombre de jeunes dorés jaunes de l'année consommés et leur abondance dans le lac démontre que la prédation par le doré noir peut être un facteur de survie important pour le doré jaune.

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DAILY feeding rates of walleye, *Stizostedion vitreum vitreum*, and sauger, *S. canadense*, in Lake of the Woods, Minnesota, were estimated to measure the influence of feeding interrelationships on walleye production. Accurate estimates of the total daily meal, diurnal feeding periodicity, and the number of each prey species consumed were determined employing the technique

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of Swenson and Smith (1973). Relationships between feeding rate and prey density were defined to determine whether food limited growth and production. In measuring the significance of predation and cannibalism in controlling food availability and walleye survival, numbers of prey species and young-of-the-year walleye consumed daily were related to the abundance of prey and young-of-the-year walleye.

Food competition between walleye and sauger in the lake was suggested by Carlander (1942) who demonstrated a high degree of similarity in diets and distribution. Both species preyed on young-of-the-year walleye and sauger. Carlander (1949) concluded that selective commercial fishing for walleye, and feeding interactions with sauger were responsible for declining walleye abundance as reflected by declining commercial catches. However, estimates of relative abundance based on catch and effort data after 1948 did not suggest a decline (Heyerdahl and Smith 1972). Comparison of walleye growth estimates calculated by Carlander (1942) and Heyerdahl and Smith (1972) showed that growth had not changed.

The inconclusive results of previous Lake of the Woods research and Larkin's (1956) review of competition research illustrate the limitation of measuring food habit, distribution, abundance, and growth to study feeding interrelationships; Ricker (1946) considered measurement of the daily meal useful to this analysis. The present study was conducted to provide information on Lake of the Woods populations and to test the effectiveness of consumption rate measurements in defining effects of feeding interactions.

Materials and Methods

Fish were collected with gillnets, experimental trawl, and commercial trawl during June–September of 1968–70 at 17 stations (Fig. 1). Analysis of prey density and feeding rates were based on catches made with a 7.6-m semiballoon trawl (2-cm^2 mesh and 0.6-cm cod liner). Standard trawls filtered an estimated 2600 m^3 of water in 7 min, travelling at 4.8 km h^{-1} (3 mph). Six hundred and eight trawls were made during 52 days with intensive sampling (19–24 h) on 19 days. Experimental trawling was done at depths from 1.3 to 8 m in areas with sand or organic bottom (Stations 1–4, 7, 9; Fig. 1). Walleyes and saugers taken from 11 m (Stations 15–17) in a commercial trawl were used in describing diets. Gillnets were set at Stations 1–14 during June, July, and September 1968–70. A total of 229 sets were made with 77 × 1.9-m (250 × 6 ft) nets consisting of five 15.4-m (50 ft) panels of 38-, 51-, 64-, 76-, and 102-mm (1.5, 2, 2.5, 3, and 4 in.) stretch mesh. Four sets were made each day at depths averaging 2, 4, 5.5, and 7.5 m to define walleye and sauger distribution. Catch per experimental trawl or gillnet set was recorded for all species. Temperatures were recorded at the fishing depth during trawling.

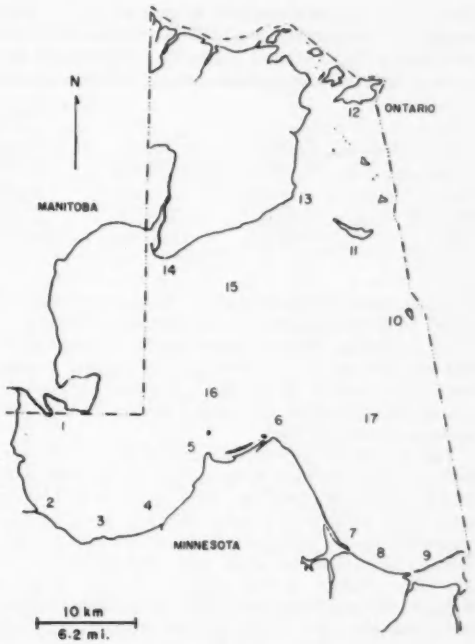

FIG. 1. Minnesota and Manitoba waters of Lake of the Woods showing location of sampling stations.

Experimental trawl catches were used as an abundance index of predator and prey populations on the assumption that walleye, sauger, and principal prey species were vulnerable to the net in proportion to their abundance. Comparison of length frequency distributions of gillnet and trawl catches showed that trawling caught walleye and sauger under 400 mm effectively. Larger walleye and sauger comprised less than 8 and 3% of the gillnet catches, respectively. Changes in total prey catch per unit of effort (CPE) generally reflected changes in abundance for trout-perch, *Percopsis omiscomaycus*, and yearling yellow perch, *Perca flavescens*, during June, and young-of-the-year yellow perch during August–September. Yellow perch and trout-perch were generally vulnerable to the trawl mesh during these periods, however, some recruitment of yellow perch probably occurred during August. Behavior and size had a significant influence on the vulnerability of less abundant species, young-of-the-year yellow perch, and trout-perch during other periods. Effectiveness of trawl catches in describing prey abundance and changes in abundance significantly limited the assessment of effects of predation on prey density. Prey counts were converted to weight from mean weights calculated twice monthly for major species and once each month for less important prey.

Stomach samples were preserved in 5–15% formalin for later identification and quantification of

TABLE 1. Average abundance of major prey species, young-of-the-year walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) during 1969–70 at depths of 1.3–5 m and 5.1–8 m described as the average of yearly mean catch per trawl. Effort and catch for depths exceeding 5 m are in parentheses.

	Sampling days	Net lifts	Catch per trawl by species and depth					Total catch ($mg\ m^{-3}$)
			Perca flavescens	*Percopsis omiscomaycus*	*Notropis* spp.	*S. vitreum vitreum*	*S. canadense*	
June	15	114(16)	2(0)	62(410)	4(0)	0(0)	0(0)	100(575)
July	9	106(11)	532(80)	86(352)	5(2)	0(0)	0(0)	205(486)
Aug.	17	128(27)	772(137)	146(639)	22(1)	2.7(0.1)	2.5(7.5)	532(689)
Sept.	9	87(20)	562(283)	190(798)	18(0)	1.9(2.1)	4.8(65.0)	616(1,008)

stomach contents. Identification of ingested fish was based on distinctive external features, bone structure, and morphology of the digestive tracts. Contents were wet weighed to 0.01 g. Diets of walleye and sauger were described as percentage frequency of occurrence and percentage by weight of prey in stomach samples containing food.

The procedure of Swenson and Smith (1973) was used to estimate food consumption of walleye and sauger exceeding 200 mm total length (TL). The total daily meal and amount of each prey species consumed by the average sauger or walleye are defined as milligrams per gram and gram per gram per day. The product of the monthly average of individual daily consumption (gram per gram per day) and average weight of walleye or sauger exceeding Age 0 in a standard trawl catch was used to estimate consumption by index populations in the 2600 m^3 sampled by a standard trawl. The number of each prey species consumed was estimated by dividing the total weight of that species by the mean individual weight. Relationships between the number of yellow perch and trout-perch consumed by index populations of walleye or sauger and the rate of decline of these species in trawl catches were used to determine the influence of predation on food supply. The influence of limited food abundance on feeding rate was determined from relationships between estimates of individual consumption (milligrams per gram per day) and prey density. The relationship between the number of young-of-the-year walleye or sauger consumed by the index populations and mean CPE of young-of-the-year was used to estimate the significance of predation on walleye abundance.

To determine if differences in the time of feeding reduced direct interaction, change in feeding intensity over 24 h was estimated from the percentage of the total meal consumed during 1 h at night, early morning, midday, and late afternoon (Swenson and Smith 1973). Estimates were limited to 15 days during which sampling was extended over 19 h and sample size exceeded 24 individuals.

Results

Distribution and Abundance of Prey

Trawl catches showed that trout-perch were the dominant species in deeper areas (5.1–8 m) throughout the summer and in shallow water (1.3–5 m) during June (t-test; $P < 0.05$; Table 1). Yellow perch were predominant from July to September in shallow water (t-test; $P < 0.05$). Emerald shiners (*Notropis atherinoides*) and spottail shiners (*N. hudsonius*) concentrated in shallow areas (t-test; $P < 0.05$) and were second in abundance during June (Table 1). In order of abundance, other prey species included johnny darter (*Etheostoma nigrum*), young-of-the year lake herring (*Coregonus artedii*), sauger, walleye, burbot (*Lota lota*), and logperch (*Percina caprodes*). All concentrate in shallow areas with the exception of young-of-the-year lake herring, sauger, and walleye.

Prey fish abundance (milligrams per cubic meter) increased significantly ($P < 0.05$) in shallow water from the end of June to September as a result of increased abundance and rapid growth of young-of-the-year yellow perch. During June the abundance of most species appeared to decline. Total prey fish density declined at a rate of 1.7 mg m^{-3} day^{-1} ($P < 0.2$). Trout-perch and yearling yellow perch declined at rates of 1.7 and 0.15 individuals day^{-1} 2600 m^{-3} ($P < 0.2$; $P < 0.1$, respectively). The June reduction in perch appeared to be a continuation of the decline which began during August of the previous year. Abundance of young-of-the-year perch declined at a rate of 19 individuals day^{-1} 2600 m^{-3} during August and September 1970 ($P < 0.05$).

Distribution of Walleye and Sauger

Gillnet and trawl catches showed concentrations of walleye (Age I and older) in shallow water during July, August, and September when prey abundance is highest ($P < 0.05$). June catches of walleye indicated a more uniform distribution with depth (Table 2). Sauger increased significantly with depth ($P < 0.05$) during August and September, but were more uniformly distributed during June and July (Table 2).

Food of Walleye and Sauger

Diets — The major increase in abundance of

TABLE 2. Average catch per standard experimental trawl tow (ET) and gillnet set (GN) of walleye and sauger in Lake of the Woods, Minnesota at four depths, during 1968–70. Number of sets is in parentheses.

	Gear	Depth (*m*)			
		1.5–3.0	3.1–4.6	4.7–6.2	6.3–10
		Walleye			
June	GN	9.5(2)	3.3(4)	6.7(3)	10.5(2)
	ET	5.1(9)	4.6(6)	4.8(4)	7.1(10)
July	GN	17.2(32)	10.1(33)	7.0(26)	5.2(27)
	ET	5.5(42)	3.3(18)	2.4(5)	2.1(8)
Aug.	ET	3.9(69)	2.7(17)	1.6(7)	0.8(17)
Sept.	GN	18.7(25)	21.2(26)	16.5(26)	14.4(23)
	ET	5.6(34)	5.2(36)	1.5(12)	2.5(14)
		Sauger			
June	GN	31.5(2)	19.4(4)	24.3(3)	29.5(2)
	ET	7.7(9)	11.0(6)	9.3(4)	3.2(10)
July	GN	26.6(32)	35.3(33)	31.0(26)	32.2(27)
	ET	10.4(42)	9.9(18)	7.2(5)	5.1(8)
Aug.	ET	7.0(68)	9.4(17)	11.0(7)	10.4(17)
Sept.	GN	3.6(25)	9.8(26)	21.1(26)	27.7(23)
	ET	2.2(34)	3.5(36)	11.6(12)	16.7(14)

young-of-the-year perch was reflected by increased occurrence of perch in diets of Age I and older walleye and sauger (Tables 3 and 4). Perch occurred in 5% of the walleye stomachs containing food during June and in 76% or more of samples collected after June. Perch occurred in 3% of sauger stomachs during June and 65% or more after June. Lower use of perch by saugers may reflect a tendency for sauger to concentrate in deep water with trout-perch which were important in their diet throughout the summer (Table 4). The use of trout-perch by walleye dropped from 10% in June to an average of 2% after June. Young-of-the-year yellow perch was the predominant prey of Age 0 walleye during August and September (Table 3). Planktonic crustaceans were the only food of Age 0 sauger (Table 4).

The importance of individual prey species was similar in the diets of walleye and sauger older than Age 0. A significant correlation ($P < 0.05$) was found between the use–rank of items in June and September diets of walleye and sauger. However, first rank items differed during June and July when prey abundance was low. Items were ranked in order of their percentage occurrence. The percentage of empty walleye stomachs decreased progressively from 31% during June to 15% in September (Table 3). A smaller decrease in the percentage of empty sauger stomachs occurred during the same period (Table 4).

Young-of-the-year sauger were eaten by walleye in September. Sauger ate yearling sauger during June–July and young-of-the-year in August–September. Young-of-the-year walleye were eaten by sauger in August (Table 4). Walleye were not cannibalistic (Table 3).

Feeding schedules — Diel feeding schedules of walleye and sauger over 200 mm TL were similar. Feeding schedules were identified for 2 days in June, 4 days in July, 5 days in August, and 4 days during September 1969–70. Feeding patterns resembled those described for the 1966 walleye year-class (Swenson and Smith 1973).

Walleye food consumption — Food consumption by walleye exceeding 200 mm TL increased from approximately 1% of body weight (10 mg g^{-1} day^{-1}) during June to 3% of body weight (30 mg g^{-1} day^{-1}) during August and September (Table 5). A curvilinear relationship (Fig. 2) between estimates of average daily food consumption for each month, and estimates of average prey density for areas less than 5 m deep, was found to be significant ($P < 0.01$). Consumption was limited by food availability during June and July when density averaged less than 300 mg m^{-3}, but was not limited at the higher August–September forage densities.

Although average consumption suggested that available food limited walleye feeding rates, daily consumption rates for a given month were inversely related to daily changes in estimated prey density; a significant negative rank correlation coefficient was found for June 1969 ($r_c = -0.70$; $P < 0.05$). The contradiction may relate to the

TABLE 3. Food of young-of-the-year (O) and older walleye (I+) expressed as percentage frequency of occurrence of stomachs containing food and in parentheses, percentage by weight.

	June (I+)	July (I+)	Aug. (O)	Aug. (I+)	Sept. (O)	Sept. (I+)
No. stomachs	301	334	95	300	12	670
Percentage empty	31	26	15	18	10	15
Annelida	—	1(<1)	—	—	—	—
Hirudinea	—	1(<1)	—	—	—	1(1)
Crustaceans	26(5)	4(5)	9(1)	2(1)	36(12)	—
Amphipoda	—	1(<1)	—	—	—	—
Cladocera	26(5)	1(<1)	4(<1)	—	36(12)	—
Decapoda	1(<1)	2(5)	—	2(1)	—	—
Copepoda	—	—	9(<1)	—	—	—
Fish	43(78)	82(70)	90(99)	100(99)	64(88)	100(100)
Perca flavescens	5(2)	76(57)	67(83)	76(81)	64(87)	93(90)
Percopsis omiscomaycus	10(13)	2(1)	—	3(1)	—	1(1)
Notropis spp.	11(16)	9(10	1(3)	4(3)	—	3(1)
Etheostoma nigrum	1(<1)	1(<1)	—	2(<1)	—	1(<1)
Coregonus artedii	15(47)	1(2)	—	6(4)	—	7(7)
Stizostedion canadense	—	—	—	—	—	4(<1)
S. vitreum vitreum	—	—	—	—	—	—
Lota lota	1(<1)	1(<1)	—	1(<1)	—	—
Percina shumardi	—	—	—	1(<1)	—	1(<1)
Unidentified	6(<1)	2(<1)	26(13)	32(9)	9(1)	7(1)
Insects	41(17)	41(24)	1(<1)	4(<1)	—	1(<1)
Ephemeroptera	38(17)	41(24)	—	4(<1)	—	1(<1)
Chironomidae	4(<1)	1(<1)	1(<1)	—	—	—
Trichoptera	—	1(<1)	—	—	—	—

fact that walleye feed more than 1.1 m from the bottom and daily fluctuations in forage abundance reflect vertical movement of food organisms into and out of the 1.1 m stratum sampled by the bottom trawl. Under these conditions forage availability for walleye would be greatest during days when forage catches were low.

Assessment of the effects of temperature on food consumption is necessary to interpret relationships between food abundance and food consumption. June and late September samples were collected at 14.5 C and late July, August, and early September temperatures averaged 20 C. Similarity of mean consumption for August (28 mg g^{-1} day^{-1}) and late September (30 mg g^{-1} day^{-1}) when food availability did not limit consumption suggests that temperature differences did not alter feeding rates. Digestion studies demonstrated that food digested per hour by walleye is positively related to stomach volume (W. A. Swenson unpublished data). The highest stomach volumes occurred in samples from late September, indicating that reductions in the digestion rate (associated with lower September temperatures) are counteracted by increased digestion associated with high stomach volumes.

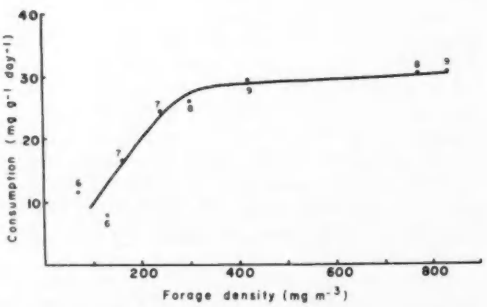

FIG. 2. Relationship of consumption by walleye (*Stizostedion vitreum vitreum*) to forage density. Numbers associated with plotted points indicate month of sampling.

Sauger food consumption — Food consumption by sauger during June 1969 was positively related to daily changes in forage density ($r_s = +.75$; $P < 0.05$). This relationship may reflect a tendency to feed closer to the bottom, an assumption supported by distribution analysis and by research demonstrating visual adaptation of sauger for lower light conditions (Ali and Anctil 1968).

TABLE 4. Food of young-of-the-year (0) and older sauger (I+) expressed as percentage frequency of occurrence of stomachs containing food and in parentheses, percentage by weight.

Item	June (I+)	July (I+)	Aug. (0)	Aug. (I+)	Sept. (0)	Sept. (I+)
No. stomachs	333	363	70	341	16	380
Percentage empty	43	40	13	30	13	38
Annelida	1(<1)	1(<1)	—	—	—	—
Hirudinea	1(<1)	1(<1)	—	—	—	—
Crustaceans	3(<1)	1(1)	100(100)	1(<1)	100(100)	—
Amphipoda	—	—	3(<1)	1(<1)	—	—
Cladocera	3(<1)	—	83(69)	—	95(98)	—
Decapoda	—	1(1)	—	—	—	—
Copepoda	—	—	60(31)	—	23(2)	—
Fish	92(99)	94(96)	—	100(100)	—	100(100)
Perca flavescens	3(1)	65(18)	—	80(59)	—	66(40)
Percopsis omiscomaycus	78(89)	38(66)	—	15(28)	—	29(28)
Notropis spp.	5(2)	4(7)	—	2(2)	—	3(2)
Etheostoma nigrum	4(3)	2(3)	—	1(<1)	—	1(<1)
Coregonus artedii	1(1)	1(<1)	—	1(2)	—	10(21)
Stizostedion canadense	1(2)	1(1)	—	1(1)	—	7(8)
S. vitreum vitreum	—	—	—	1(1)	—	—
Lota lota	—	1(1)	—	1(3)	—	—
Percina shumardi	—	—	—	1(<1)	—	—
Unidentified	12(1)	1(<1)	—	15(5)	—	5(<1)
Insects	9(1)	8(3)	—	—	—	—
Ephemeroptera	8(<1)	8(3)	—	—	—	—
Chironomidae	1(<1)	1(<1)	—	—	—	—
Trichoptera	—	—	—	—	—	—

TABLE 5. Mean daily food consumption of walleye and sauger exceeding 200 mm TL. Consumption is expressed as weight consumed (grams) and weight consumed per gram of fish weight (milligrams per gram). Standard deviation of mean estimates are given in parentheses.

	No. days	No. fish day^{-1}	Mean fish wt (*g*)	Consumption (*g*)	Consumption (*mg g*$^{-1}$)
			Walleye		
June 1969	9	21	219	2.5(1.4)	11.6(6.7)
June 1970	2	44	272	2.0(0.6)	7.5(2.7)
July 1969	2	57	223	3.7(0.6)	16.5(0.8)
July 1970	3	46	322	7.8(1.7)	24.6(6.8)
Aug. 1969	1	48	334	7.1(—)	30.3(—)
Aug. 1970	2	46	351	8.8(6.1)	26.0(20.8)
Sept. 1969	2	65	306	9.2(2.6)	30.5(10.7)
Sept. 1970	6	55	388	11.3(4.6)	29.2(11.3)
			Sauger		
June 1969	7	25	172	3.0(2.3)	16.8(12.5)
June 1970	2	39	194	4.4(1.0)	22.3(2.6)
July 1969	2	71	171	2.0(0.4)	11.8(2.1)
July 1970	3	38	185	3.9(2.7)	20.7(13.3)
Aug. 1969	1	81	161	4.2(—)	26.6(—)
Aug. 1970	2	52	199	3.7(2.5)	17.6(9.7)
Sept. 1969	1	31	183	3.5(—)	19.1(—)
Sept. 1970	6	29	225	3.6(1.5)	16.0(7.8)

TABLE 6. Estimated number of prey consumed daily by index populations of walleye and sauger in Lake of the Woods, Minnesota.

Period	Catch consumption by species					
	Perca flavescens	*Percopsis omiscomaycus*	*Notropis* spp.	*C. artedii*	*S. canadense*	*S. vitreum vitreum*
			Walleye			
June 1969	0.32	0.13	0.40	0.31	—	—
June 1970	—	0.54	—	0.06	—	—
July 1969	47.18	0.05	0.34	0.04	—	—
July 1970	28.10	0.03	0.58	0.03	—	—
Aug. 1969	37.88	—	0.78	0.09	—	—
Aug. 1970	25.31	—	0.13	0.05	—	—
Sept. 1969	17.49	—	0.03	0.12	—	—
Sept. 1970	24.45	0.04	0.14	0.15	0.02	—
			Sauger			
June 1969	0.05	1.51	0.12	0.04	—	—
June 1970	—	7.23	0.08	—	0.07	—
July 1969	32.68	2.28	0.34	0.10	—	—
July 1970	11.85	5.76	0.10	—	0.20	—
Aug. 1969	30.54	2.27	0.45	—	—	0.14
Aug. 1970	12.99	2.36	0.20	—	—	—
Sept. 1969	0.21	1.32	0.05	0.08	—	—
Sept. 1970	2.18	1.46	0.30	0.49	0.30	—

Daily estimates of consumption were variable and means for August and September did not exceed those for June and July (Table 5). Average daily consumption by sauger was not influenced significantly by changes in mean prey density ($P < 0.1$).

PREDATION AND PREY ABUNDANCE

Consumption of prey by index populations of walleye and sauger in shallow water (< 5 m) was compared with rates of decline in prey abundance. Consumption of perch by walleye during June 1969 was 0.3 individuals day^{-1} (Table 6) which exceeds the 0.15 individuals day^{-1} 2600 m^{-3} calculated rate of decline of yellow perch. Sauger consumed 1.5 trout-perch day^{-1} (Table 6) which approximates the estimated decline of 1.7 individuals day^{-1} 2600 m^{-3} in trout-perch abundance. The calculated rate of decline of 19 individuals day^{-1} 2600 m^{-3} in young-of-the-year yellow perch for August and September was exceeded by estimated walleye consumption of 25 individuals day^{-1} 2600 m^{-3}. Consumption of perch by sauger approached that of walleye during August, but was greatly reduced during September when sauger moved into deep water. Recruitment of young-of-the-year yellow perch to August trawl catches would result in underestimates of the rate of decline and appears responsible for differences between predation estimates and estimated rate of decline in perch abundance.

Consumption of young-of-the-year sauger by walleye during September at the rate of 0.02 individuals day^{-1} 2600 m^{-3} represented 0.2% of the average daily young-of-the-year sauger catch in water less than 5 m. Sauger from both deep and shallow areas consumed 0.7% of the estimated total young-of-the-year sauger population during September 1970. Predation by sauger on young-of-the-year walleye during August 1970 was equivalent to 0.14 individuals day^{-1} 2600 m^{-3} or 5.2% of the estimated population 2600 m^{-3}. Based on the number of days predation occurred, the estimates indicate walleye and sauger ate approximately 20% of young-of-the-year sauger available during September 1970 when the abundance of young-of-the-year, predation, and cannibalism were greatest. Calculated predation by sauger on young walleye exceeded 100% of the estimated index population for August 1969.

An analysis of commercial CPE presented by Heyerdahl and Smith (1972) for the period 1949–70 showed that abundance of walleye and sauger fluctuates greatly but has not declined. Fluctuations were related to changes in strength of recruiting year-classes. The greatest recruitment of walleye and sauger to the commercial fishery occurs at Ages VI and VII, respectively (Heyerdahl and Smith 1972). On the basis of

these observations, effects of cannibalism by sauger were tested by correlating abundance during a given year with abundance 5, 6, and 7 yr later and with the means for these years. Effects of predation by walleye on young-of-the-year sauger were tested by adjusting for the 1-yr difference in recruitment. Coefficients obtained in all tests were insignificant and give no indication that predation by older age-groups determined success of sauger year-classes. Appropriate tests to determine effects of predation by sauger on survival of young-of-the-year walleye produced similar results. Year-class strength of walleye and sauger were positively correlated ($r = +0.57$; $P < 0.01$), demonstrating that unidentified factors are of primary importance in controlling relationships between walleye and sauger year-classes.

Growth of Walleye

Food consumption, growth, and food conversion efficiency were described for the large 1966 walleye year-class by Swenson and Smith (1973). Growth was slowest during the June–July period of low prey abundance. Growth defined as the product of food consumption and conversion efficiency averaged 2.3 mg g^{-1} day^{-1} during June 1969, and 4.5, 5.9, and 6.4 mg g^{-1} day^{-1} for July, August, and September 1969–70, respectively. Growth in June was 59% less, and in July 20% less, than estimates for the August–September period of high food availability.

Discussion

The similar food habits of walleye and sauger, and the relationship between walleye feeding rates and forage density indicate a demand for food in excess of supply during June through July and hence interspecific food competition as defined by Larkin (1956). Relationships between consumption by index populations and changes in prey abundance show predation by walleye and sauger represents the principal factor controlling food availability. Predation by walleye appeared to be the major cause of yellow perch mortality during June, August, and September. Predation by sauger was a factor controlling abundance of trout-perch during June and abundance of yellow perch during August through September. Utilization of yellow perch during August and September occurred under conditions of unrestricted food supply and did not represent direct competition; however, predation during this period appeared to be the cause for limited availability of yellow perch and food competition during the following June.

Although the study was useful in establishing the existence, cause, and temporal extent of food competition, the differences in distribution, diets, and potential for growth compensation prevented our isolating the effects of interspecific competition with sauger from intraspecific food competition, and accurately measuring the influence of food competition on walleye growth. Partial segregation by depth was demonstrated by net catches during this study and an earlier survey (Carlander 1942; 1944). Differences in strata occupied during feeding were identified by correlating estimated daily feeding rates with estimates of prey density, and by differences in walleye and sauger diets. Walleye demonstrated a tendency to occupy shallower strata and feed on pelagic prey in contrast to sauger which showed a stronger association with deeper strata and trout-perch. These differences were reflected in the relative effects of predation by walleye and sauger on prey populations, and demonstrate that intraspecific competition is most significant in limiting food availability, food consumption, and growth of walleye.

Growth compensation has been identified in young-of-the-year walleye (Smith and Pycha 1960) and can be expected to occur where food availability changes from the limiting, to the unrestricted condition within the growing season. Reduction in growth during the June–July food limiting period may have been compensated by increased feeding and growth during the August–September period of unrestrictive food availability. Feeding and growth compensation would magnify differences between feeding rate and growth estimates defined for the June–July and August–September periods, while reducing the effects of food competition. Because August and September growth compensation would not completely compensate for effects of food competition occurring during June and July (Smith and Pycha 1960), reduction in walleye growth probably results from intra- and interspecific food competition.

Analysis of commercial CPE did not indicate that predation by sauger, or cannibalism, influenced walleye survival, although relationships between the number of young-of-the-year walleye consumed by sauger, and abundance of young walleye suggested that predation is a limiting factor. The contrasting results are believed to be associated with precision of the testing procedures and sample size. Because effects of unidentified factors on relationships between walleye and sauger year-class strength could not be isolated, the analysis based on commercial CPE provided limited information on predation. Feeding studies showed young-of-the-year walleye were

rare in the diet of sauger. However, when considered at the population level, predation appeared highly significant to survival due to the relatively high predator abundance and low young-of-the-year walleye abundance. Estimates of predation rate and the abundance of young-of-the-year walleye differed, which suggests that sampling was inadequate to quantify accurately the effects of predation. Failure to demonstrate the existence of walleye cannibalism reported by Carlander (1942) may also result from inadequate sampling. Studies of mortality, diets, and abundance of walleye and prey populations by Forney (1971, 1976) showed predation and cannibalism by walleye are important in controlling walleye and yellow perch year-classes in Oneida Lake. Our analysis demonstrated that estimates of food consumption can be used to define effects of predation and cannibalism. However, more intensive sampling will be necessary to quantify accurately the influence of predation by large populations of predators on the survival of low density prey such as young-of-the-year walleye.

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Community and Species Responses of Chironomidae (Diptera) to Contamination of Fresh Waters by Crude Oil and Petroleum Products, with Special Reference to the Trail River, Northwest Territories

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ROSENBERG, D. M., AND A. P. WIENS. 1976. Community and species responses of Chironomidae (Diptera) to contamination of fresh waters by crude oil and petroleum products, with special reference to the Trail River, Northwest Territories. J. Fish. Res. Board Can. 33: 1955–1963.

On oiled and unoiled artificial substrates in the Trail River, Northwest Territories, communities of Chironomidae were different during open-water periods but were similar over the winter. Greater numbers of species and individuals of Orthocladiinae occurred on the oiled than on the unoiled artificial substrates. The reverse was true for Tanypodinae and Chironominae. Ten species of Chironomidae showed a positive response to the presence of oil, 9 species showed a negative response, and 10 species were apparently unaffected. Based on the results of this study and a literature review, 11 species of Chironomidae showing either positive or negative responses to contamination by oil or petroleum products were evaluated for their potential to indicate oil contamination of freshwater ecosystems. Three criteria were used: taxonomic soundness, wide zoogeographic distribution, and numbers in the community. We predict that *Nilotanypus fimbriatus* (Walk.), *Cricotopus bicinctus* (Meig.), and *C. varipes* Coq., individually or as an assemblage, would fulfill this role.

ROSENBERG, D. M., AND A. P. WIENS. 1976. Community and species responses of Chironomidae (Diptera) to contamination of fresh waters by crude oil and petroleum products, with special reference to the Trail River, Northwest Territories. J. Fish. Res. Board Can. 33: 1955–1963.

Sur des substrats artificiels avec ou sans pétrole de la rivière Trail, Territoires du Nord-Ouest, les communautés de Chironomidae diffèrent quand l'eau est libre de glace, mais sont semblables en hiver. Les Orthocladiinae sont plus nombreux tant en espèces qu'en individus dans les substrats artificiels avec pétrole que sans pétrole. On observe le contraire pour les Tanypodinae et les Chironominae. Dix espèces de Chironomidae manifestent une réponse positive à la présence de pétrole, 9 espèces une réponse négative et 10 espèces semblent inaffectées. En nous basant sur les résultats de cette étude et sur une revue de la littérature, nous avons évalué le potentiel, comme indicateur de contamination d'écosystèmes d'eau douce par le pétrole, de 11 espèces de Chironomidae montrant des réponses soit positives soit négatives à la contamination par le pétrole ou par les produits pétroliers. Nous avons utilisé trois critères: solidité taxonomique, répartition géographique étendue, et nombres dans la communauté. Nous sommes d'avis que *Nilotanypus fimbriatus* (Walk.), *Cricotopus bicinctus* (Meig.) et *C. varipes* (Coq.), individuellement ou en groupe, pourraient jouer ce rôle.

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THERE is little information on ecological consequences of accidental oil spills into freshwater ecosystems. By comparison, studies on effects of marine oil pollution are relatively well advanced. Contemporary exploration and development of oil reserves in arctic North America (including potential overland transport of crude oil in pipelines) together with an overall increase in human activity north of 60° lat. will almost certainly lead to increased exposure of northern rivers and lakes to contamination by petroleum products. Therefore, it is essential to determine responses of northern freshwater ecosystems to oil contamination to develop guidelines to control this problem.

The studies of Dickman (1971), Hutchinson et al. (1972), Hutchinson and Hellebust (1974), and Roeder et al. (1975), among others, provide an information base on the responses of northern freshwater algae to oil contamination. In the present study, we investigate responses of larval Chironomidae to experimental contamination of

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artificial substrates and review results of recent field studies involving effects of oil and petroleum products on Chironomidae in fresh waters.

Study Area and Methods

The Trail River enters the Mackenzie River about 50 km downstream from Fort Simpson. Ranges of physical and chemical parameters of Trail River water are given in Brunskill et al. (1973). Experimental work was done at 62°06′ N, 122°11′ W on the river, <1 km above its confluence with the Mackenzie River. The Trail here is a sequence of pools (1–1.5 m deep) and riffles (.5–1 m deep) with a width of approximately 15 m; substrate is mainly 15–50-cm boulders with fine and coarse sand and gravel. To our knowledge, the river had not been previously contaminated by oil or petroleum products.

The artificial substrates (AS) used were chicken barbecue baskets (Anderson and Mason 1968) filled with 30–35, 5–8-cm diam stones, mainly granite and andesite, taken from dry areas of the riverbank. Artificial substrates were immersed in Norman Wells crude oil (supplied by Imperial Oil Ltd.), excess oil was allowed to drain off, and the AS were placed in pools and staked to the river bottom. Unoiled AS were installed upstream of the oiled to avoid contamination by oil. Sufficient numbers of experimental and control AS were installed in 1972 and 1973 to ensure that three of each could be removed per sampling. Statistical analysis previously done showed no significant difference in numbers of macrobenthos between AS in a set of three (Snow and Rosenberg 1975b). At least 1 mo was allowed between installation and the first sampling. We originally intended to sample approximately monthly during open water and every 2 mo during the period of ice cover. However, ice >2 m thick prevented sampling in January and March 1973. Instead, these AS were removed in June 1973 along with normally scheduled sets for that date (Table 1).

One rock, selected at random, was removed from each AS after it was dipped in the crude oil (prior to installation in the river) and, subsequently, whenever AS were removed. Adhering oil was extracted according to Brunskill et al. (1973) to determine amounts of oil and rates of oil loss. Oil did not soak into the rocks.

Removal of AS from the river and zoobenthos from the rocks, and preservation and enumeration of zoobenthos were described in Brunskill et al. (1973). All nets and sieves used were 200-μm mesh. Immature Chironomidae were usually given species designations. Species identifications were made when possible.

Chironomid communities were characterized by the diversity index $\bar{d}$ (Margalef 1958; Wilhm and Dorris 1966). Tests done on numbers of invertebrates of various taxa (mainly family, genus, and species) on nine AS removed in June 1973 showed that the asymptote of diversity (Wilhm 1970) was reached in the first sample for the unoiled AS and after the third successively pooled sample for the oiled AS. Therefore, we considered that three AS of each type were sufficient to give a stable $\bar{d}$ value for the Chironomidae. Kendall's τ coefficient (Siegel 1956; Ghent 1963) was used as an index of similarity for comparing communities of Chironomidae on oiled and unoiled AS.

To characterize responses of individual species of Chironomidae to the presence of crude oil, total numbers of individuals of a species in three replicates each of oiled and unoiled AS were used. A maximum of 16 occurrences (8 oiled, 8 unoiled) were possible. Species occurring from 12 to 16 times ($\geq$75 to 100% occurrence) were assigned to Group I; from 8 to 12 times ($\geq$50 to <75% occurrence), Group II; from 4 to 8 times ($\geq$25 to <50% occurrence), Group III. Species of Chironomidae in the 0 to <25% occurrence group were excluded as being too erratic for patterns of response to the crude oil to be characterized. Next, within each group, three responses were identified: 1) positive — numbers higher on oiled than on unoiled AS in more than half the occurrences; 2) negative — numbers higher on unoiled than on oiled AS in more than half the occurrences; 3) unaffected — numbers higher on either unoiled or oiled AS in approximately half the occurrences. Finally, the "positive" and "negative" responses were subdivided into "strong" (87.5–100% occurrence) and "moderate" (75–87.4% occurrence). Responses that could be characterized as "weak" never occurred and so this subdivision was omitted. To analyze responses of species of Chironomidae quantitatively on several sampling dates and verify placement of species into strong or moderate response categories, a paired-difference t-test (Snedecor and Cochran 1967) was used. Oiled and unoiled AS were considered to be nonindependent because they were placed in the same habitat. The paired-difference t-test was done on total numbers of individuals of a species of Chironomidae on three oiled and three unoiled AS. A log + 1 transformation was used on the data. The following arbitrary classification of responses was made using significance levels of the t values: strong, $\geq$95%; moderate, $\geq$90 to <95%; unaffected, $\leq$90%.

Results

Estimated oil residues on the oiled AS ranged from 378.6 to 12075.0 mg and were detectable throughout the period of study. Initial total weights of oil (8042.7, 12075.0, and 11193.0 mg) were similar for the three dates of installation (Table 1). However, for the only comparable colonization periods (28 and 56/57 days), residues declined faster on AS installed on July 12, 1973 than on those installed on July 14, 1972 because discharge of the river during the 1973 28- and 57-day colonization periods was higher (Table 1). Total annual discharge of the river in 1973 was estimated to be 69.5×10^6 m^3, over twice that of 1972 (26.6×10^6 m^3). We are unable to explain the low percent of oil remaining on AS colonized for 132 days after July 14,

TABLE 1. Norman Wells crude oil residues on rocks in oiled artificial substrates (AS) placed in the Trail River, N.W.T.[a] NA = not applicable; * set A; + set B.

Date AS installed	Colonization period (*days*)	$\bar{x}$ River discharge for colonization periods indicated[b] ($m^3\ s^{-1}$)	$\bar{x}$ (±1 SD) concn of oil (*mg oil/g rock*)	Estimated total wt of oil on AS[c] (*mg*)	% oil remaining on AS
July 14, 1972	0	NA	1.34(.70)	8,042.7	100.0
	28	2.3	1.51(.59)	5,588.3	69.5
	56	1.6	.45(.25)	2,665.8	33.2
	132		.05(.007)	378.6	4.7
	335		.31(.11)	2,278.5	28.3
September 8, 1972	0	NA	1.36(.53)	12,075.0	100.0
	279*		.34(.11)	3,400.8	28.2
	279+		.06(.018)	534.3	4.4
July 12, 1973	0	NA	1.56(.54)	11,193.0	100.0
	28	2.8	.33(.12)	3,161.7	28.3
	57	2.5	.16(.17)	1,764.6	15.8

[a]Oil residues were below detectable levels on rocks from unoiled AS.

[b]Means not given for colonization periods >57 days because insufficient winter data were collected.

[c]Calculations based on mean weight (milligrams) of oil per rock × 35, the approximate number of rocks per AS.

TABLE 2. Characterization of Chironomidae communities on oiled (O) and unoiled (U) artificial substrates (AS) in the Trail River, N.W.T. A, during the open water periods and B, over winter. Diversity index value = $\bar{d}$.

Dated AS installed	Colonization period (*days*)	No. species		No. individuals		$\bar{d}$		τ corrected	Kendall's τ *P*	Are the communities similar?[a]
		O	U	O	U	O	U			
A. July 14, 1972	28	17	19	648	316	1.36	2.05	.254	.099	No
	56	21	27	7523	610	.94	2.31	.258	.038	No
	132	20	22	8610	2062	.92	2.23	.144	.312	No
July 12, 1973	28	12	16	1987	995	.95	1.87	.314	.060	No
	57	21	18	1501	532	1.54	1.37	.015	.912	No
B. July 14, 1972	335	26	24	924	973	1.69	2.28	.233	.057	No
Sept. 8, 1972	279									
Set A		26	24	869	696	2.54	2.03	.582	<.00006	Yes
Set B		23	27	848	793	2.49	2.29	.509	.0001	Yes

[a]Decision based on $P \leq .01$.

1972 (4.7%) and set B colonized for 279 days after September 8, 1972 (4.4%) (Table 1).

Communities of Chironomidae colonizing oiled and unoiled AS are characterized in Table 2. For the open-water sets, the number of species of Chironomidae was slightly higher on unoiled (range: 16–27) than oiled AS (range: 12–21) in four out of five colonization periods. However, at least twice the number of individuals colonized oiled (range: 648–8610) than unoiled AS (range: 316–2062) (Table 2A). Values of $\bar{d}$ varied from .92 to 1.54 for communities on oiled AS, from 1.37 to 2.31 on the unoiled and were higher for unoiled in four of the five colonization periods. This indicates a more equitable distribution of numbers of individuals among species on the unoiled AS. Values for Kendall's τ showed that the communities of Chironomidae colonizing the oiled and unoiled AS were dissimilar.

Differences between communities of Chironomidae on AS over winter were not as pronounced. Numbers of species and individuals were not significantly different for oiled or unoiled AS (Table 2B). Values of $\bar{d}$ were higher on the oiled (1.69, 2.54, 2.49) than the unoiled AS (2.28, 2.03, 2.29) for two of the three sets. Kendall's τ showed that two of the three sets had similar communities (Table 2B).

Responses of the three subfamilies of Chironomidae found on the AS are shown in Table 3. The Orthocladiinae tended to have more species on oiled than on unoiled AS. The reverse was

TABLE 3. Responses of subfamilies of Chironomidae to contamination of artificial substrates (AS) in the Trail River, N.W.T., by crude oil.[a]

Subfamily	Times no. of species were highest			Times mean no. of larvae were highest		
	Oiled AS	Unoiled AS	Tied	Oiled AS	Unoiled AS	Inconclusive[b]
Tanypodinae	1	4	3	2	3	3
Chironominae						
Chironomini	2	4	2	2	4	2
Tanytarsini	1	4	3	2	4	2
Orthocladiinae	4	2	2	8	0	0

[a]For the eight sampling times in the study.
[b]Only one value for oiled or unoiled AS.

TABLE 4. Responses to crude oil of species of Chironomidae in Groups I (≥75 to 100% frequency of occurrence), II (≥50 to <75% frequency of occurrence), and III (≥25% to <50% frequency of occurrence). (For fractions in parentheses: numerator is the number of times the species occurred in higher numbers on oiled artificial substrates than on unoiled for a "positive" response and vice versa for a "negative" response. Denominator is the number of occurrences of the species out of a maximum of eight possible dates. The first fraction in parentheses in the "unaffected" group is the number of times the species occurred in higher numbers on oiled artificial substrates than on unoiled; vice versa for the second fraction.)

Positive			Negative	
Strong	Moderate	Unaffected	Moderate	Strong
		GROUP I		
Conchapelopia spp. (8/8)		*Nanocladius* sp. *2* (4/7 & 3/7)	*Rheotanytarsus* sp. *1* (6/8)	*Corynoneura* n.sp. (8/8)
Cricotopus bicinctus[a] (Meigen) (8/8)		*Polypedilum* sp. *4*[b] (4/8 & 4/8)	*Thienemanniella* n.sp. (6/8)	*Nilotanypus fimbriatus* (Walker) (7/8)
C. varipes Coq. (7/8)		*Rheocricotopus* sp. *2* (4/7 & 3/7)		*Paratendipes* sp. *1* (7/7)
Eukiefferiella paucunca Sæther (7/8)				
Eukiefferiella sp. *1* (7/8)				
		GROUP II		
Orthocladius (*Euorthocladius*) n. sp. (5/5 & 1 tie)	*Eukiefferiella claripennis* (Lundbeck) (4/5)	*Micropsectra* sp. *1* (4/7 & 3/7)		*Synorthocladius* n.sp. (7/7 & 1 tie)
		Polypedilum laetum (Meigen) (3/5 & 2/5)		
		GROUP III		
Orthocladius sp. *3* (4/4)	*Brilla* sp. *1* (5/6)	*Eukiefferiella* sp. *8* (2/3 & 1/3)		*Constempellina* sp. *2* (3/3)
Parakiefferiella sp. *1* (5/5)		*Microcricotopus* sp. *1* (1/3 & 2/3 & 1 tie)		*Stempellinella* sp. *1* (4/4 & 1 tie)
		Microspectra sp.2 (2/3 & 1/3)		Tanypodinae Gen. B (2/2)
		Paraphaenocladius sp. *2* (2/5 & 3/5)		
		Phaenopsectra sp. *3* (2/3 & 1/3)		

[a]After completion of this manuscript, we (unpublished data) found a new species of *Cricotopus* among the *C. bicinctus* from the Trail River. Using larval instar data to separate the two species and to estimate the numbers of larvae of each species on oiled and unoiled artificial substrates, we found no change in the response status of *C. bicinctus*. Moreover, *Cricotopus* n.sp. also belongs to Group I and showed a strong, positive response to the contamination of artificial substrates by crude oil. These new data will not significantly alter conclusions reached in this paper.
[b]*Polypedilum ophioides* (Meigen) and *Polypedilum* n.sp. nr. *illinoense* in approximately equal proportions.

true of the Tanypodinae and Chironominae. The latter two subfamilies tended to have higher mean numbers of individuals on unoiled AS but the Orthocladiinae clearly had higher mean numbers of individuals on oiled AS.

Responses of species of Chironomidae in Groups I, II, and III are shown in Table 4. In all, 10 species responded positively and 9 species negatively to the oil. Ten species were apparently unaffected. Except for *Conchapelopia* spp., all positively responding species were Orthocladiinae. In the negative group, the distribution was: three species of Orthocladiinae, four species of Chironominae and two species of Tanypodinae. In the

unaffected group there were equal numbers of species of Chironominae and Orthocladiinae. Results of the paired–difference *t*-tests agreed well with the original classification of Chironomidae responses. Only four discrepancies occurred. We have not corrected Table 4 because of the relatively minor nature of the changes suggested by results of analysis of the quantitative data.

Discussion

Crude oils and oil products persist in the environment (Blumer and Sass 1972). Therefore, it is not surprising that we detected residues of crude oil on rocks of the oiled AS almost a year after application. Moore and Dwyer (1974) noted that weathering processes significantly alter composition of oil in the environment, causing wide variations in biological effects. We agree that biological effects of oil contamination vary over time but feel that response of the macrobenthic community is an integration of these effects over the period of study. Moore and Dwyer (1974) listed five classes of effects of oil on marine organisms. Over a relatively long period of time, such as was involved in our study, only one of these classes, alteration of habitat, is pertinent.

Unoiled rocks did not support appreciable algal growth but oiled rocks supported a macroscopic algal community (Roeder et al. 1975). Unfortunately, quantitative data were not obtained. However, our field observations indicated that most algal growth occurred after 28, 56, and 57 days of colonization in 1972 and 1973. Stimulation of plant growth by the presence of oil has been reported elsewhere as well (Roeder et al. 1975).

Increases in periphytic algal biomass on oil-contaminated AS may be due to: 1) reduction in numbers or elimination of zoobenthic grazers by toxic fractions of the crude oil allowing algal growth far in excess of normal; or 2) nutrients supplied by the oil stimulating algal growth. Both these hypotheses need to be tested experimentally. Our observations in the Trail River indicate that herbivorous Chironomidae were unaffected by the crude oil. We suggest that nutrients supplied by the oil stimulate algal growth and that the algae attract more Chironomidae, particularly Orthocladiinae which are usually associated with such habitats (Thienemann 1954; Learner et al. 1971; Janković 1973; Roback 1974).

Oiled and unoiled AS left over the winter showed inconsistent differences in numbers of species, numbers of individuals, and values of $\bar{d}$ and Kendall's τ (Table 2B) probably because lower oil residues remaining on the AS due to longer exposure to the river water and because the period spent under deep ice and snow resulted in reduction or elimination of the algal community. (Note that the only two sets of AS which, according to Kendall's τ, had similar communities of Chironomidae on oil-treated and control AS, were installed on September 8, 1972, after the period of maximal algal growth and just prior to freeze-up).

Of the community parameters used, number of individuals and Kendall's τ provided the strongest evidence that communities of Chironomidae colonizing oiled and unoiled AS from open-water periods were different. These two parameters may be the most useful ones in future work of this type.

Data on responses of species of Chironomidae to the presence of oil never showed that one species occurred exclusively either on oiled or on unoiled AS so we assumed that oil treatment did not completely exclude (or exclusively encourage) the occurrence of a species. Therefore, relegation of species to Groups II and III when they belonged in Group I did not occur. Theoretically, species present in positive and negative categories of Groups II and III were as responsive as those in Group I. However, on a practical basis, it is better to use a consistently present species to judge an impact than one which occurs intermittently. This use eliminates the need to explain presence or absence on the basis of factors other than the impact being studied. Furthermore, relative abundance of indicator species to the rest of the community is important (Brinkhurst and Cook 1974). This approach would answer objections to the use of indicator species on a presence or absence basis (e.g. Roback 1974). Therefore, the positively and negatively responding species of Group I should have the greatest potential to be "indicator species," individually or as a group.

We examined results of a number of field studies for responses of Chironomidae to contamination of freshwaters by oil and petroleum products. The U.S. Environmental Protection Agency (1973) report of an accidental spill of 7000 U.S. gal of No. 2 diesel fuel into Boone Creek, South Carolina, included species identifications of Chironomidae. We reevaluated the raw data for Chironomidae given in the Boone Creek report for comparison with the Trail River results. Using the same terminology as in the Trail River study, seven species were designated as positive responders and four as negative responders (Table 5). The Boone Creek data were too inconclusive for "strong" or "moderate" categories or inclusion of an unaffected group. As in the Trail River study, Orthocladiinae were the

TABLE 5. Reevaluated responses of Chironomidae in the Boone Creek Oil spill study (U.S. Environmental Protection Agency 1973). Species with comments a and c could be considered strong responders relative to the other species in this table.

Positive		Negative	
Species	Comment	Species	Comment
Conchapelopia sp.	—[a,b]	*Arctopelopia* sp.	
Cryptochironomus fulvus — complex		*Tanytarsus* (= *Rheotanytarsus*) *exiguus* (Johannsen)	—[c,d]
Polypedilum fallax (Johannsen)		*Polypedilum* (*Pentapedilum*) *tritum* (Walker)	
Cricotopus bicinctus (Meigen)	—[a,e]	*Metriocnemus* (= probably *Parametriocnemus*) sp.	
Cricotopus slossonae (Malloch)	—[a,f]		
Nanocladius (= probably *Eukiefferiella*)			
Nanocladius (= *Microcricotopus*) *alternantherae* Dendy and Sublette			

[a]Occurred in at least two of three sample types in vastly higher numbers at downstream stations.
[b]Occurred in all sample types upstream and downstream. Downstream outnumbered upstream 36 specimens to 3.
[c]Occurred in at least two of three sample types in vastly higher numbers at upstream stations.
[d]Occurred in three sample types upstream and one downstream. Upstream outnumbered downstream eight specimens to one. (This may be highly significant in terms of the higher number of downstream stations considered than upstream).
[e]Occurred in all sample types downstream but none upstream. Number of specimens downstream = 35.
[f]Occurred in two sample types downstream but none upstream. Number of specimens downstream = 27.

commonest positive responders to the effects of the oil spill (Table 5). *Cricotopus bicinctus* (Meigen) and *Conchapelopia* spp. responded positively in both studies (Tables 4, 5). Diesel fuel was detectable in sediments, flora, and fauna of the affected part of Boone Creek throughout the study and an increased growth of periphyton occurred at stations downstream from the oil spill (U.S. Environmental Protection Agency 1973). As in the Trail River, increased occurrence of Orthocladiinae may have been a response to increased algal growth caused by the presence of diesel fuel.

Snow and Rosenberg (1975a) reported the effects on littoral zoobenthos of an experimental oil spill of 409 liters of Norman Wells crude on a lake in the Mackenzie Delta. Crude oil residues were detectable in littoral sediment for 15 mo after the spill. Periphytic, filamentous blue-green algae increased during the open-water season following crude oil addition. A decrease in abundance of Chironomini and Tanytarsini and an increase in abundance of Orthocladiinae resulted after the oil spill. *Cricotopus* sp. 6 (=*C. varipes* Coq.) was common to the Trail River and the Delta lake. It showed a positive response to the addition of crude oil in the lake (Snow and Rosenberg 1975a) and was a "strong positive" responder in the Trail River study (Table 4).

Use of species assemblages or entire communities of benthic invertebrates to indicate environmental disturbances in freshwater ecosystems is currently favored over the use of single species (Gaufin 1973; Roback 1974). No matter which is used, the concept of indicators may be made more useful by rigidly defining criteria for their use.

One of the most successful uses of zoobenthos as indicators has been the lake typological systems of Brundin (1956) and Sæther (1975). We propose that at least the following three criteria, similar to those used in lake typology work, be used for designating species of Chironomidae indicators of environmental change due to human interferences:

1) Taxonomic soundness — The species should be "good" (i.e. no disagreement as to its status and not a member of a species complex) and should have reasonably distinct characteristics for ease of identification.

2) Wide distribution — It or an ecologically similar sister species should have a wide zoogeographic distribution so it is useful, predictively, as an indicator over wide geographic areas.

3) Abundance — It must be numerous in the community before the impact occurs. (Rationale for this criterion has been discussed above).

We used these criteria to predict the usefulness of species of Chironomidae as indicators of oil contamination (Table 6). Of the 11 species listed, we consider that *Nilotanypus fimbriatus* (Walker), *C. bicinctus*, and *C. varipes*, individually or as an

TABLE 6. Evaluation of some species of Chironomidae as potential indicators of oil-contaminated ecosystems. (Species considered are those from published reports reviewed here as well as the Trail River study. The three criteria used are explained in detail in the text.)

Species	Reference	Response designation	Agreement with criteria			Predicted usefulness as indicator species
			Taxonomically sound	Wide distribution	Numerous	
Nilotanypus fimbriatus (Walker)	this study	negative (strong)	Yes (Fittkau 1962; Roback 1971). The genus is monospecific in North America so identification of immatures does not pose a problem.	Yes, Nearctic (Roback 1971). Also *N. dubius* (Meigen) is a sister species with a widespread European distribution (Fittkau 1962).	Yes (this study)	high
Rheotanytarsus exiguus (Johannsen)	U.S.E.P.A. (1973)	negative	Likely but published information is scanty. Larvae of *Rheotanytarsus* are difficult, if not impossible, to identify; *R. exiguus* is one of the commonest species of *Rheotanytarsus* in North America so immatures of *Rheotanytarsus* will probably be *R. exiguus* but not with complete certainty.	Yes. Nearctic (Sublette and Sublette 1965). O. A. Sæther has extended the range to Manitoba (unpublished data).	Not in U.S.E.P.A. (1973). Their net spinning mode of life may restrict them to specialized habitats	low
Polypedilum fallax (Johannsen)	U.S.E.P.A. (1973)	positive	Yes (Townes 1945). However, immatures can only be identified to *fallax* group (= 10 species).	Yes. Nearctic (Townes 1945)	Not in U.S.E.P.A. (1973) but generally recognized as being numerous (e.g. see Townes 1945).	moderate
P. (Pentapedilum) tritum (Walker)	U.S.E.P.A. (1973)	negative	Yes (Townes 1945). However, immatures can only be identified to subgenus.	Yes. Holarctic (Townes 1945)	Yes, in Townes (1945). However, not in U.S.E.P.A. (1973) and Lake Winnipeg (O. A. Sæther unpublished data).	moderate
Cryptochironomus fulvus – complex	U.S.E.P.A. (1973)	positive	No. As it now stands, this complex contains several species and is in need of revision. Adults cannot be identified, some larvae can, and pupae can.	Yes. Nearctic (Townes 1945)	Not in U.S.E.P.A. (1973) but generally recognized as being numerous (e.g. see Townes 1945).	low
Cricotopus bicinctus (Meigen)	this study, U.S.E.P.A. (1973)	positive (strong)	Yes (Hirvenoja 1973)	Yes. Holarctic (Hirvenoja 1973)	Very (Thienemann 1954; Roback 1957; Surber 1959; Learner et al. 1971; U.S.E.P.A. 1973; Hirvenoja 1973; this study).	very high
C. slossonae Malloch	U.S.E.P.A. (1973)	positive	No. Larvae and pupae appear to be identical to those of *C. varipes*. Females of *C. slossonae* and *C. varipes* differ only in minor leg coloration (O. A. Sæther personal communication). Therefore, *C. slossonae* could be a synonym of *C. varipes*.	Fairly. Reported from the eastern half of the USA (Sublette and Sublette 1965).	Not usually (Roback 1957) but was the second commonest *Cricotopus* in U.S.E.P.A. (1973) although found in low numbers.	low
C. varipes Coquillett	this study, Snow and Rosenberg (1975a)	positive[a]	Yes (Sublette 1966). Immatures are not yet described but are easily identified. *C. tristis* Hirvenoja may be a color variety and a junior synonym (O. A. Sæther personal communication).	Nearctic. From N.W.T. to Florida. (Sublette and Sublette 1965; this study). *C. tristis* is a sister species with a northern European distribution (Hirvenoja 1973).	Yes (this study; O. A. Sæther unpublished data from Lake Winnipeg).	high
Nanocladius alternantherae Dendy and Sublette	U.S.E.P.A. (1973)	positive	Yes (Dendy and Sublette 1959). Immatures are probably easily identified.	No. Restricted to southern USA (Sublette and Sublette 1965).	Not in U.S.E.P.A. (1973)	low
Eukiefferiella claripennis (Lundbeck)	this study	positive (moderate)	Yes (Lehmann 1972). The pupa is easily identified but the larva is difficult.	Yes. Holarctic (Sæther 1969, as *E. hospita* Edwards).	Can be (Brundin 1949) but not consistently numerous in this study.	moderate
E. paucunca Sæther	this study	positive (strong)	Probably (Sæther 1969); *E. paucunca* is very similar to *E. calvescens* Edwards, a European species. The pupa is easily identified but the larva is difficult.	Nearctic (Sæther 1969); *E. calvescens*, a sister species, has a widespread European distribution (Lehmann 1972).	Yes (this study). Learner et al. (1971) reported *E. calvescens* to be abundant in the upper, cleaner part of the river of their study.	moderate

[a]Showed a strong positive response in this study but not in Snow and Rosenberg (1975a).

assemblage, will best indicate contamination by oil and petroleum products. Numbers of *N. fimbriatus* should be depressed by the presence of oil and petroleum products while numbers of the other species should be increased, relative to control areas. *Cricotopus bicinctus* is capable of responding to a number of different environmental contaminants (Surber 1959; Learner et al. 1971; Mason et al. 1971) so, if it is to be useful as an indicator of oil contamination, evidence supporting the presence of oil or petroleum products should be sought.

Levels of contamination that will cause responses in certain species within the benthic community are difficult to identify. Massive oil spills will be detrimental to the entire benthic community. Such spills are so obvious that the use of indicator species is unnecessary. Small spills or low-level chronic contamination by oil or its derivatives may not be obvious because of dissolution (e.g. see Lysyj and Russell 1974; Sniegoski 1975; Harrison et al. 1975) or spreading (European Petroleum Organizations 1974). Studies considered here (U.S. Environmental Protection Agency 1973; Snow and Rosenberg 1975a; and the Trail River) involve small or small to medium spills according to a classification proposed by European Petroleum Organizations (1974).

Many biological field studies involving responses of the benthic community to accidental contamination by oil or petroleum products lack quantitative data on amounts of contaminant involved. Such information is necessary if we are to quantify responses of benthos. Even if quantitative data on the amount of oil spilled are available, these data are usually not presented in a biologically meaningful manner. Should the amount be expressed as a concentration (milligrams per liter, milligrams per gram, parts per million), an absolute quantity (tons, kilograms, liters) or a quantity per unit length or area of the affected site (kilograms per kilometer of shoreline, kilograms per square kilometer of bottom)? Clearly, this is a future research need.

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Theoretical Effect of Schooling by Planktivorous Fish Predators on Rate of Prey Consumption[1]

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EGGERS, D. M. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. J. Fish. Res. Board Can. 33: 1964–1971.

Effect of schooling on the rate of prey consumption by planktivorous fish is deduced by extending the Holling disk equation (i.e. the rate of prey consumption by solitary feeding fishes can be expressed by the Holling disk equation) to account for lateral visual-field overlap and reduction of prey density due to removal of prey by forward-occurring members of the school. Effect of schooling is expressed as the rate of prey consumption per member of the school relative to that by a solitary individual. This study suggests that schooling of predators occurs at the expense of prey consumption. Cost of schooling is reduced if prey densities are high, if distance between members is high, or if school size is small. There may be some advantage to schooling when prey have a clumped distribution.

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Une extension de l'équation discoïde de Holling a servi à déduire l'effet de la formation de bancs sur le taux de consommation des proies par des poissons planctophages (i.e., le taux de consommation des proies par des poissons se nourrissant solitairement peut s'exprimer par l'équation discoïde de Holling), dans le but d'expliquer le chevauchement du champ visuel latéral et la diminution de la densité des proies par suite de leur enlèvement par les membres qui se trouvent en tête du banc. L'effet de la formation de bancs est exprimé comme taux de consommation des proies par membre du banc relativement à celui d'un individu solitaire. Les résultats de cette étude donnent à croire que la formation de bancs chez les prédateurs se fait au dépens de la consommation des proies. Le coût de ce comportement diminue quand la densité des proies est élevée, la distance entre les membres est grande ou le banc est petit. Il peut y avoir certains avantages à la formation de bancs quand les proies sont groupées en masses compactes.

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THERE is considerable literature regarding schooling in fishes which has been largely summarized by Radakov (1973). Much of the literature assumes that schooling results from comparatively simple sensory responses of individual fish (Parr 1927). Many authors have endeavored to determine these responses, largely through laboratory studies. Among other things they show that fish schools are highly structured and stable. This information provides the necessary postulates concerning the structure of fish schools from which relevant ecological implications can be deduced. It is the objective of this paper to deduce the effect of schooling on the rate of prey consumption by planktivorous fish. The approach is to begin with a model that predicts the rate of prey consumption by a solitary-feeding planktivore. This model is then extended, assuming some well-defined structure for the fish school, to account for competition for prey among members of the school.

Intuitively, one would expect the amount of food ingested to be less for schooled planktivores because of competition between individual members of the school whose visual fields overlap. This mutual sharing of visual fields results in a lower rate of prey encounter per unit time for schooled fish than for nonschooled fish which possess an identical stationary visual field. The extent of encounter rate reduction depends upon the distance separating nearest neighbors of the school relative to the distance at which prey are detectable as well as the explicit structure (expressed as a sphere packing scheme) of the fish school. A second consequence of fish schooling

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is that prey density relative to individual members is not constant over the length of the school. Rather, prey density decreases as one progresses from the anterior to the posterior end of the school (relative to the direction of school movement), owing to removal of zooplankton from the water column, which are encountered first by fish at the front of the school (O'Connell 1972). I subsequently show through a rigorous treatment of the above-mentioned processes that the expected food consumed by schooling planktivores exploiting a randomly distributed prey population is substantially less than that consumed by solitary-feeding planktivores exploiting the identical prey population.

Theoretical Derivation of Effects of Schooling on Rate of Prey Consumption

The following derivation requires a model giving the explicit structure of the school as well as a model giving the rate of prey consumption by solitary-feeding fish.

Breder (1959) provided a working definition of a fish school. A school is a group of individuals oriented in one direction, at the same distance apart, and moving at the same speed. The school is maintained through forces of attraction and repulsion among the individuals that vary with the distance between individuals (Breder 1959; Hemmings 1966). The school then is an equilibrium realization of these forces.

Cullen et al. (1965) and Pitcher (1973) have modeled the structure of fish schools based upon various sphere packing schemes used in the study of crystal lattice structure. Although fish are constantly changing their location in the school relative to other members, the structure nevertheless exists in a statistical sense. Thus, the structure of the school is dynamic rather than fixed. Cullen et al. (1965) examined the three-dimensional structure of pilchard (*Harengula* sp.) schools. These schools tend to have a body-centered cubic lattice structure, with each individual having eight nearest neighbors located at the vertices of a cube surrounding the individual. Pitcher (1973) found that the minnow *Phoxinus phoxinus* formed schools close to the sphere packing based upon aggregating regular tetrahedra. In this case, each individual has 12 nearest neighbors located at the vertices of a regular icosahedron. School structure analogous to various close packing schemes used in the study of crystal lattice structure assumes a spherical free space around the fish. Van Olst and Hunter (1970) found that in four species of marine pelagic fishes the distance between an individual and the neighbor directly anterior was less than the distance between the individual and its lateral neighbors. This suggests that the free space is ellipsoidal rather than spherical.

In the derivation of the effect of schooling, I assume the least compact school structure, so as to provide a meaningful upper bound on reduction of foraging success due to schooling. If a less compact school structure occurs, then it would follow that foraging success would be higher. Consider the following assumptions:

1) Each member of the school is assumed to have eight nearest neighbors located at the vertices of a cube (body-centered cubic packing) surrounding the individual. This is the least compact structure reported in the literature, assuming a spherical free space.

2) The nearest neighbor distance is defined to be the distance between the center and the vertices of the cube. This implies that any school structure with ellipsoidal free space, where the minor axes lie in the direction of movement, would be more compact.

3) The school is assumed to be of sufficient size that the number of individuals located on the periphery of the school is small compared to the total number of individuals in the school. Thus, the bias accrued to peripheral individuals having less visual-field overlap is negligible. Under the above assumptions, the school can be specified by two parameters: the distance between nearest neighbors and the length of the school in the direction of movement.

The following derivation assumes that the planktivore visually encounters and pursues individual prey from a single-species prey population of uniform size. Rate of prey consumption by a solitary feeding planktivore can be expressed by the Holling disk equation (Holling 1959):

$$C = \frac{\lambda \cdot N}{1 + \lambda \cdot N \cdot TH} \qquad (1)$$

where C is the rate of prey consumption, λ is the visual field volume per unit search time, N is prey density, and TH is the prey handling time. The visual field is assumed to be approximated by a cylinder of radius equal to the maximum lateral distance of prey visibility (Eggers 1977; Confer and Blades 1975).

The visual field for any individual member of the school is identical with that of members that occur directly in front of or directly behind that individual, on the line of school movement, because these individuals ultimately swim through the same volume of water column in a period of foraging time. Thus, the visual fields of individuals occurring on the same line of school movement do not instantaneously overlap. Effect

of competition between members along the line of school movement is a decrease in prey density along this line, owing to prey removal by forward members along the line.

Competition for prey also exists between a given individual and those that occur lateral to the direction of movement. The visual field of a given individual overlaps simultaneously with those members occurring laterally. Since prey encounter is a Poisson stochastic process (discussed in Eggers 1977), any fishes that share their visual fields have an equal probability of eating any prey that occur in the mutual visual field. This effect can be specified theoretically by reducing the potential visual field cross-sectional area of solitary predator to an effective visual field cross-sectional area adjusted for overlap with lateral-occurring members of the school.

I assume that the school structure is such that each individual potentially shares its visual field cross-sectional area with each of its eight nearest neighbors. With this assumption I am ignoring lateral visual-field overlap with members that occur in body-centered cubic subunits other than that in which the individual is contained. Relaxing this assumption greatly complicates computing the degree of visual-field overlap, and as shown later, ignoring this further interaction results in only a slight bias in estimating the actual lateral visual-field overlap.

Effect of schooling on prey consumption is expressed as a response to those parameters which characterize the school. The nature of the response is elucidated by a computer program which varies the nearest neighbor distance and length of the school, and for each parameter combination calculates the ratio of prey consumed while feeding in a school to prey consumed while feeding as a solitary predator.

The effective cross-sectional area of the visual field is based upon the intersection of five circles whose radius is the maximum lateral distance of prey visibility. The centers of the circles are at the vertices and center of a square. This simple configuration is derived from the projection of the cylindrical visual field of each individual of the body-centered cubic subunit on a plane perpendicular to the direction of school movement. In calculating the effective cross-sectional area, one simply partitions the visual field of the central member of the subunit into areas shared by 1, 3, 5, 7, and 9 individuals (including the central member). The effective cross-sectional area (CS) then is a weighted sum of these areas.

$$CS = A_1 + \frac{A_3}{3} + \frac{A_5}{5} + \frac{A_7}{7} + \frac{A_9}{9} \qquad (2)$$

where A_i is the total area shared by i individuals. With the body-centered cubic arrangement of individuals in a school, there exist four possible partitionings of shared areas. These together with the conditions that bring them about are shown in Fig. 1. Thus, the encounter rate adjusted for lateral visual-field overlap is the product of the effective cross-sectional area and the swimming speed.

The effective visual field calculated in the above manner, in theory, is not shared simultaneously by other members of the school. Thus, there is no direct interference due to view blockage by other members. However, an individual prey may be attacked by more than one fish. The above theory does not consider the time spent pursuing prey that are ultimately captured by other members of the school. If multiple attacks of the same prey individual occur, then prey handling time (on the average) is higher than that of solitary-feeding fish. This further reduces the average

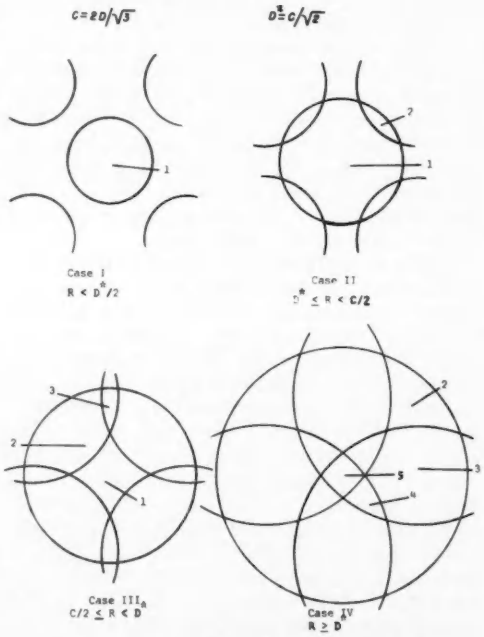

FIG. 1. Projection of the visual fields of each member of the cubic subunit onto a plane perpendicular to the direction of school movement. D is the nearest neighbor distance, D^* is the nearest neighbor distance projected onto a plane perpendicular to the direction of movement, C is length of a side of the cubic subunit, R is the radius of the visual field of a solitary fish. Areas 1, 2, 3, 4, 5 are shared by 1, 3, 5, 7, 9 individuals, respectively.

rate of prey consumption relative to the rate of solitary-feeding fish.

Effect of school size on foraging success need only be assessed for each "row" of the school because the school consists of a number of rows, each of the same length and individual encounter rate. The visual field (expressed as volume per time) of a given individual is exploited by all members occurring in front of that individual. The zooplankton density relative to any given individual must be adjusted for that exploitation.

To find this zooplankton density, consider the following. Suppose the prey population consists of one species of constant size, the predator pursues all prey individuals as encountered, and prey that are pursued are captured and eaten. Then the predicted number of prey consumed (C_i) by the ith individual in the row (individual 1 is the most forward occurring member) is:

$$C_i = \frac{\lambda^* \cdot N_i}{1 + \lambda^* \cdot N_i \cdot TH} \tag{3}$$

where λ^* is the adjusted encounter rate, N_i is the zooplankton density relative to the ith individual, and TH is the handling time for each pursuit initiated. The zooplankton density changes according to

$$\frac{dN_i}{dt} = -\frac{C_i}{\lambda^*} \tag{4}$$

The average food consumed is calculated using a finite difference approximation to N_i and C_i, that is,

$$C_i = \frac{\lambda^* \cdot N_{i-1}}{1 + \lambda^* \cdot N_{i-1} \cdot TH} \tag{5}$$

$$N_i = N_{i-1} - \frac{C_{i-1}}{\lambda^*} \tag{6}$$

where N_i is the ambient zooplankton density in the water column.

The analysis presented assumes that the prey average 1 mm long, have a copepod body form, have water-column density of 5 individuals/liter. Parameters of the predator are: the fish are 6 cm long; forage at 1 length/s; the lateral sighting distance of a prey object is 11 cm; time necessary to pursue, capture, and eat an individual prey is 0.03 min. Note the parameters that specify the predators are consistent with those estimated by fitting a similar predator–prey model to the experimental data published by Brooks (1968). Details are presented in Eggers (1977).

Output from the program that determines effect of schooling on foraging success include the following graphs. The solid curve in Fig. 2 shows the increase in encounter rate (expressed as percent of encounter rate of a solitary predator) with increase in distance between nearest neighbors. This curve was generated assuming that no lateral visual-field overlap occurs among individuals of separate subunits. Figure 3 shows the decrease in zooplankton density and the predicted food consumption as the distance from the forward end of the school increases. The curves shown in Fig. 3 were derived assuming no lateral visual-field overlap and reflect only the effect of prey removal by forward members of the school. Figure 4 shows the response surface over the parameters that characterize the school. Prey consumed by fish foraging in a school is determined by averaging over all members of the school. The response (z-axis) is expressed as a percent of food consumed by fish foraging as a solitary predator. The x-axis represents the length of the school (number of individuals). The y-axis represents the distance to the nearest neighbor (multiple of body length). Figure 4 shows the interaction of the effects of lateral visual–field overlap and prey removal by forward members. Note that the reduction of foraging success is much greater when the size of the school is large and the distance between individual members is small.

Discussion

Several simplifying assumptions were necessary for computing the effect of schooling on prey

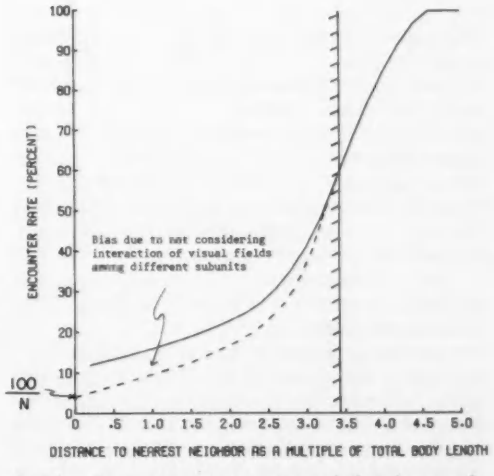

FIG. 2. Encounter rate (percent of that for a solitary predator) vs. the distance between nearest neighbors in the fish school (number of body lengths).

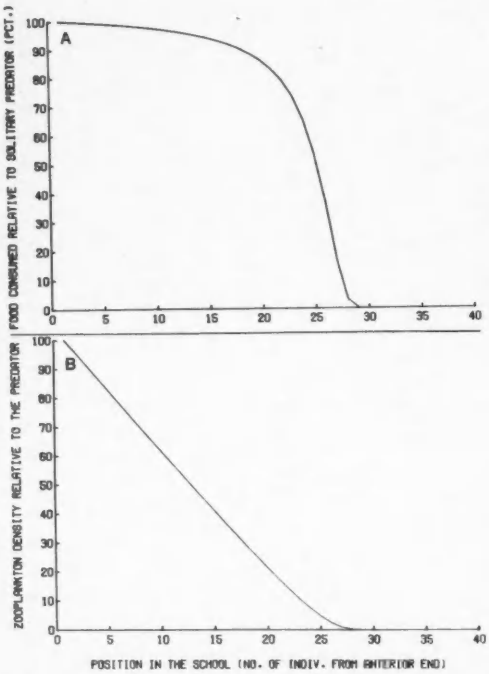
A
B
FOOD CONSUMED RELATIVE TO SOLITARY PREDATOR (PCT.)
ZOOPLANKTON DENSITY RELATIVE TO THE PREDATOR
POSITION IN THE SCHOOL (NO. OF INDIV. FROM ANTERIOR END)

FIG. 3. Foraging success relative to that of A, a solitary predator (percent) for an individual member of the school and the B, zooplankton density relative to individual members of the school (expressed as a percent of the ambient water-column density) vs. the position of the member in the school (number of individuals from the forward end of the school).

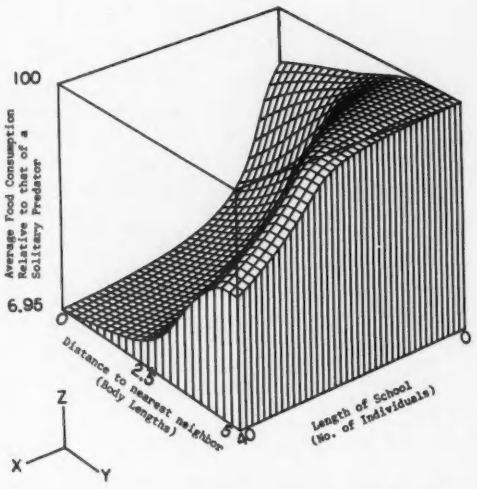

FIG. 4. Response of food consumption achieved by schooling predators averaged over all members of the school (percent of that achieved by a solitary feeding fish) to the dimensions of the fish school.

consumption. The most unrealistic assumptions were: 1) There is no visual field overlap among individuals of different subunits. 2) The arbitrary choice of model parameter values (i.e. water-column prey density, length of the fish, foraging speed of the fish, prey handling time, and the lateral sighting distance of the prey). 3) The prey population consists of a single species of uniform size. 4) The prey population has a random distribution in the water column.

The following discussion considers biases and possible incorrect conclusions resulting from these assumptions.

The assumption of no lateral visual-field overlap among individuals of different subunits is certainly incorrect. In the case considered, if the distance to the nearest neighbor is < 3.4 body lengths, then the visual field of any individual overlaps the visual field of individuals in different subunits. It is difficult to calculate the adjusted encounter rate because of the difficulty of calculating directly areas of the visual field shared by individuals in different subunits. However, it is possible to construct a lower bound on the amount of reduction in the encounter rate due to visual-field overlap.

There is a minimum distance between neighbors in fish schools. This can be inferred from Breder's (1959) mechanisms regarding attractive and repulsive forces which bring about and maintain fish schools. Breder (1965) showed that members maintain minimum distances between themselves because turbulence produced by tail beats of swimming fishes greatly interfered with locomotor efficiency of other fishes in the vicinity of the turbulence.

At this minimum distance between nearest neighbors, the visual field of any individual overlaps with a finite number of individuals because the radius of the visual field is limited. Thus, the visual field overlaps with at most n individuals. At the limiting case where the distance between nearest neighbors is zero, the visual fields overlap completely. The effective cross-sectional area is $1/n$ times the cross-sectional area of the visual field of the solitary predator. This provides a point to which the curve can be extrapolated and a lower bound on the reduction in encounter rate due to lateral overlap of visual fields. The extrapolated curve is presented in Fig. 2 as the dashed curve. Note that the shaded area represents the region in which the "true" curve must lie.

The response of foraging success to nearest neighbor distance and school size depends heavily

on particular values of prey sighting distance and water-column prey density. Are the values of prey sighting distances and prey densities from which the above response (Fig. 4) were derived realistic?

The smallest nearest neighbor (D_{min}) so that there is no lateral visual-field overlap is proportional to the lateral prey sighting distance (R). In particular,

$$D_{min} = \sqrt{6} \cdot R \quad (7)$$

In the case presented, D_{min} equals 27 cm or 4.5 body lengths. Confer and Blades (1975) have shown that R for small freshwater zooplankton ($\sim$ 1 mm long) by pumpkinseed (*Lepomis gibbosus*) is 5–15 cm; R for large freshwater zooplankton (2.5–3.5 mm long) by sunfishes (*Lepomis* spp.) is $>$ 50 cm (Werner and Hall 1974; Confer and Blades 1975). The value for R used here (11 cm) is perhaps low. For cases where R is high, D_{min} would also be high.

Van Olst and Hunter (1970) have reviewed the literature that attempts to measure the distance between nearest neighbors in fish schools. They reported that in all cases except one (16 of 17), the distance is $<$ 2.5 body lengths, and in most cases (11 of 17), the distance is $<$ 0.5 body length. These distances may be underestimated by as much as 20% because of bias inherent in the method of measuring the nearest neighbor distance (Symons 1971; J. R. Hunter personal communication). Nevertheless, the ranges of nearest neighbor distances reported in the literature suggest that lateral visual-field overlap occurs in schooling fishes.

Keenleyside (1955) reported that threespine sticklebacks (*Gasterosteus aculeatus*) school more tighly when well fed than when hungry. If hungry, the sticklebacks spread apart and become more active. Hunter (1966) showed that jack mackerel (*Trachurus symmetricus*) schools become more compact following feeding, then expand during the period of food deprivation. This behavior implies that schooling fishes may disperse (if sufficiently hungry) to minimize lateral visual-field overlap.

The amount of food consumed is relatively insensitive to prey densities above threshold levels (Fig. 3). This is consistent with the functional response of predators to prey density (Holling 1966). Once the prey density falls below this threshold, prey consumption from the front to the back decreases markedly with further decreases in prey density. Whether the school can reduce the ambient prey density below this threshold density depends on the visual-field volume and the initial prey density. This most likely occurs in situations where lateral visual-field overlap occurs or initial prey densities are low. If prey density is high or school size is small, then the effect of schooling on prey consumption is less.

The results presented assume that the predator exploits a simple prey population. It is straightforward to extend the analysis to more complicated prey populations. In more complicated situations, the prey are likely to differ in size, and therefore, radii of the visual fields for these various prey are different (Eggers 1977). The amount of overlap in visual-field and resultant reduction in prey encounter rate are different for each prey type. The magnitude of encounter-rate reduction is greater for larger and more visible prey. Also, those rarer or larger items of prey will be removed from the water column more quickly than the smaller or more abundant prey, as the larger forms are usually selected (in theory) not only because they are more visible but also are preferred because of their higher energy content. The density of the rarer forms is usually below the threshold density; therefore, they disappear rather quickly from the diet as one progresses from the front to the back of the school.

Because of these effects, the patterns of food selection are likely to be different in schooled and solitary fish. Differences in the rate of encounter of large and small prey will be less because of the compensating effect of greater lateral visual-field overlap for large prey. Nevertheless, because of food selection, the relative abundance of preferred forms and nonpreferred forms should, in theory, change over the length of the school owing to preferential removal from the water column. There should, in theory, be a greater occurrence of nonpreferred prey in the diet of posterior members of the school. This effect may persist so that the preferred forms are absent from the diet of those members occurring in the posterior end of the school. If the position of individual members in the school is changing, then on the average there will be greater occurrence of nonpreferred prey in the diet.

O'Connell (1972) has demonstrated a similar pattern of prey selection by schooling northern anchovies (*Engraulis mordax*). He showed that the percentage of biting responses decreased from the front to the back of the school. The biting response occurs instead of the filtering response if the concentration of adult *Artemia* relative to *Artemia* nauplii is above a threshold. Presumably, predation by anchovies reduced the concentration of adult *Artemia* below the threshold for biting. Initial concentration of adult *Artemia* was $<$ 0.2

individuals/liter. Therefore, O'Connell's results are consistent with those presented here.

It is necessary to consider the effects of schooling in devising sampling schemes to assess food selection. Application of the predator–prey model to data collected from schooled fish is not likely to fit predicted diet composition if the model assumes solitary configuration of the predator.

An implicit assumption of the theory is that the prey have a random water-column distribution. This is a rather arbitrary and unrealistic assumption. The theory breaks down if prey are assumed to occur in patches because the formulation of prey encounter is different for a patchy prey population. If one is to assess the effect of schooling on prey consumption, given that the prey occur in a patchy or clumped distribution, the exact mathematical distribution of the prey needs to be known. One can consider two cases in which the nature of prey patchiness can be defined, with naturally occurring patchy distributions of zooplankton probably lying somewhere between these cases.

In the first case the zooplankton are assumed to occur in patches characterized by a uniform density of prey, where there is a gradual transition between patches so that a fish predator cannot recognize the patches. The area of transition between patches must be small compared to the area of the patch, or the patch may not be characterized by uniform prey density. In the second case the zooplankton occur in clumps of high density, and the water between patches is void of zooplankton. In this case the patch is analogous to a quasi organism which can be seen at distances substantially greater than a solitary prey.

If prey are in patches of the first type, then schooling fish do not have any greater chance than a solitary fish of encountering patches of high density. Effects of schooling on foraging success would be similar to that derived with the assumption of a random prey distribution if prey had a patchy distribution of the first type. The key to this argument is that the predator cannot distinguish patches.

If the prey had a patchy distribution of the second type, schooling would have a different effect on food acquisition. To study this on a theoretical basis, one must rigorously characterize the prey distribution. It is necessary to consider the size and number of individuals per clump (i.e. whether the patches are of uniform size and density, whether the clumps themselves occur randomly or in a contagious distribution, and finally the density of patches in the water column). Since the clumps are encountered as units by the predator, I must consider what factors influence the rate of patch encounter.

Effect of schooling on foraging success would apparently depend heavily on the nature of prey clumping. Schooling would increase foraging success under some circumstances and under others decrease it.

Specific mechanisms to consider in developing a suitable theory to ascertain the effects of schooling on foraging success in which prey are assumed to have a patchy water-column distribution are the trade-offs between the following effects: 1) Schooled predators have a greater chance than individual fish of encountering a patch of prey. 2) An individual fish would have a greater chance of satiating itself than a schooled fish, given that a patch of prey is encountered.

Schooled predators have a greater chance than individual fish of encountering a patch of prey because the total visual field of the school is certainly greater than that of an individual fish. Given patch encounter, the school consumes the patch and resumes searching or satiates itself. On the other hand the volume of water searched by a number of schooled fish is less than the volume of water searched by an equal number of solitary fish, due to visual field overlap in schooled fish. Therefore, more patches would be encountered by the solitary fishes. However, the total number of prey consumed may be smaller for the solitary population because the individual fish may become satiated and consume only a limited component of the total patch that is encountered.

For schooling to be an advantage in foraging, the patches must be large enough so that the entire school can get an adequate ration even though the expected number of encounters is less. Further, if the patches are large and numerous each solitary predator is likely to encounter a patch. In this situation, the expected food consumed for schooled and solitary predators would be the same.

Under circumstances where the patches were large, it would be advantageous for the schools to disperse so as to minimize the overlap in the visual field yet maintain visual contact with other members. This behavior would increase the probability of patch encounter. Because visual contact between members of the school is maintained, members not in visual contact with the patch of prey can nevertheless find the patch from observing behavioral cues from other members of the school.

If the patches were small, then the school would have to encounter a large number of patches for all members to receive an adequate ration. The advantage derived from receiving stimuli from other members is less when patches are small.

One can consider the degree of contagion de-

creasing as one progresses from a highly clumped prey distribution to a random prey distribution. Certainly, the costs of schooling expressed as decrease in foraging success increase as the degree of contagion in the distribution of the prey population decreases.

This study suggests that schooling behavior, a mechanism reducing the chance of being preyed upon (Brock and Riffenburgh 1960), occurs at the expense of foraging efficiency. The theory also shows that it would be advantageous for schooling fishes to disperse while feeding to minimize lateral visual-field overlap. This cost of schooling behavior is less when prey densities are high, and perhaps schooling has some advantage with respect to prey consumption if the prey have a highly contagious distribution.

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Feeding Modes and Prey Size Selection in the Alewife (*Alosa pseudoharengus*)[1]

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JANSSEN, J. 1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). J. Fish. Res. Board Can. 33: 1972–1975.

Alewives (*Alosa pseudoharengus*) feed on zooplankton in three modes: 1) particulate feeding on individual prey; 2) filtering with the mouth held agape, accompanied by strong swimming; and 3) gulping, in which the mouth opens and closes more slowly than a particulate feeder and more rapidly than a filterer, and swimming is slower than in a filterer. Individuals that feed by filtering are not size selective; gulpers are size selective; and particulate feeders are more size selective than gulpers. Gulpers and filterers take more than 1 prey per mouth opening and closing; particulate feeders take only 1.

JANSSEN, J. 1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). J. Fish. Res. Board Can. 33: 1972–1975.

Le gaspareau (*Alosa pseudoharengus*) se nourrit de zooplancton de trois manières: 1) absorption de particules, proies individuelles; 2) filtrage avec bouche grande ouverte et nage rapide; et 3) avalement d'une bouchée, au cours duquel la bouche s'ouvre et se ferme plus lentement que dans l'alimentation particulaire et plus rapidement que dans le filtrage. Les individus qui se nourrissent par filtrage ne sont pas sélectifs quant à la taille des proies; les gobeurs le sont; et ceux qui se nourrissent de particules sont plus sélectifs que les gobeurs. Les gobeurs et les filtreurs saisissent plus de 1 proie à chaque ouverture et fermeture de la bouche; ceux qui se nourrissent de particules n'en saisissent que 1.

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INTEREST in size-selective predation by fish on zooplankton was largely initiated by Brooks and Dodson's (1965) studies on the effects of alewives (*Alosa pseudoharengus*) in some Connecticut lakes. The alewife is a recent invader of the upper Great Lakes and has affected the zooplankton of Lake Michigan by cropping off the larger species (Wells 1970). Brooks (1968) briefly described the behavior of alewives feeding on prey one at a time and established that they were size selective. My observations indicate that the alewife has two other feeding modes: one I will term "filtering", the other "gulping." In this paper I describe the behaviors and determine whether filtering and gulping are size selective.

Materials and Methods

Alewives were collected from Lake Michigan in the vicinity of Milwaukee, Wis., by dipnets and electroshock during summer 1975. Fish were maintained in a circular tank 2.44 m diam and 0.45 m deep (2.1 m^3). Twelve alewives (size 49–180 mm) were maintained from August 24 to September 7, 1975 on *Daphnia pulex* (some *Chaoborus* present). I report on the feeding behavior of these 12 fish but my observations are supplemented by observations on about 20 others kept with the 12 prior to August 24. I observed fish from behind a cardboard screen at the tank's edge and noted their feeding behavior and relative size. Fish were starved on September 5 and 6, and on September 7 all fish were fed *Daphnia* for 5 min, killed, body wall cut, and preserved in 10% Formalin. Water temperature was 19 C. After the test, 10, 100 ml water samples were taken from various depths and locations. Samples were not taken before to avoid disturbing the alewives. *Daphnia* were killed in MS-222® (ethyl *m*-aminobenzoate methanesulfonate) collected on a fine mesh screen, and preserved in 10% Formalin. All *Daphnia* in the water samples were counted and measured (length exclusive of spine). For fish, all *Daphnia* were counted and a random sample of 200 was measured except for the three smallest fish as none contained over 89 prey. *Chaoborus* were counted but not measured.

Results and Discussion

Prey distribution in the test tank was patchy. Counts from water samples ranged from 10 to 40

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TABLE 1. Feeding mode, total length and weight, number and dry weight of *Daphnia* consumed for experimental alewives. F = filtering; G = gulping; P = particulate feeding; s = small; vs = very small.

Fish	Total length (*mm*)	Feeding mode	W (*g*)	No. *Daphnia*	W *Daphnia* (*g*)
1	180	F	33.9	4372	0.02962
2	178	F	26.8	4095	0.02851
3	152	G	22.5	1103	0.01365
4	150	G	17.1	931	0.01491
5	134	G	15.4	1420	0.01954
6	124	G	12.7	940	0.01473
7	114	Ps	12.9	663	0.01537
8	110	Ps	10.9	696	0.01427
9	100	Ps	8.0	595	0.01434
10	71	Pvs	1.3	66	0.00141
11	51	Pvs	0.7	44	0.00067
12	49	Pvs	0.6	89	0.00176

(median = 26; mean = 25.4 [254,000/m^3]). Variance was 101.67 yielding a coefficient of dispersion (variance/mean) of 4.0 indicating a contagious distribution (Sokal and Rholf 1969).

Different-sized fish displayed different feeding behavior. The six smallest fish (49–114 mm) displayed a behavior which I term "particulate" feeding. The fish swims horizontally, then, as prey are encountered, the head is tipped up to suck in prey. Mouth opening and closing is very rapid. Brooks (1968) observed that alewives took only one prey at a time and my own observations indicated that fish oriented to individual prey. Filtering was characterized by swimming with the mouth fully agape for about 0.5–2 s while driving hard with the tail. After the filtering bout, the fish briefly coasts or swims slowly until the next bout which usually follows immediately. This behavior was similar to that described for the northern anchovy (*Engraulis mordax*) by Leong and O'Connell (1969). The two largest fish fed by filtering (178–180 mm). The third behavior is intermediate between particulate feeding and filtering, and I term it "gulping." The gulping alewives continuously opened and closed their mouths at a much slower rate than a particulate feeder (maximum of 2–3 times/s) but the fish did not hold its mouth open nor drive hard as a filterer does. Gulping usually came in bouts of several gulps, followed by a pause of about 0.5 s, then another gulping bout. The four medium-size fish (124–152 mm) fed by gulping. Neither gulpers nor filterers tipped the head up while feeding. Particulate feeders seldom opened the mouth completely to suck in prey; gulpers and filterers fully opened the mouth. Particulate feeders altered course for each prey, feeding on prey one at a time; filterers did not alter course for individual prey but sometimes swam in circles or figure eights in an area 20–40 cm diam and probably concentrated on patches of high prey density. Gulping fish appeared intermediate in behavior and mostly swam in an unaltered course but its gulps appeared directed, probably at select prey.

Conditions eliciting these behaviors depended on prey size and density and fish size. Smaller prey and higher densities elicit gulping and filtering. I have observed filtering most often in large fish (>170 mm) at densities of 100 or more *Daphnia pulex* per liter; medium fish (120–160 mm) gulp, and small fish (<120 mm) feed particulately. Filtering is not exclusive to large fish; I have observed filtering behavior in alewives 50–70 mm when fed high densities of diatoms (mainly *Tabellaria*, density not measured). Large fish also feed by particulate feeding when prey is large (*Mysis*, *Pontoporeia*) or prey is small but not very dense.

Table 1 gives the total lengths and weights of experimental fish, feeding mode, number and dry weight of *Daphnia* consumed. Figure 1 summarizes the size distribution (in percent) of *Daphnia* in the test water and in fish stomachs. Each histogram pools the fish that fed in a particular mode. Particulate feeders were divided into small and very small fish as none of the very small fish consumed over 89 prey. Arrows denote median prey size for individual fish.

The size distribution of the prey consumed by each of the filterers did not differ from the sample distribution for Fish 1 ($P > 0.50$) and Fish 2 ($P > 0.25$) (Chi-square goodness of fit test, Sokal and Rohlf 1969). All other fish had a distribution significantly different from the samples and filterers ($P < 0.001$ in each case) indicating

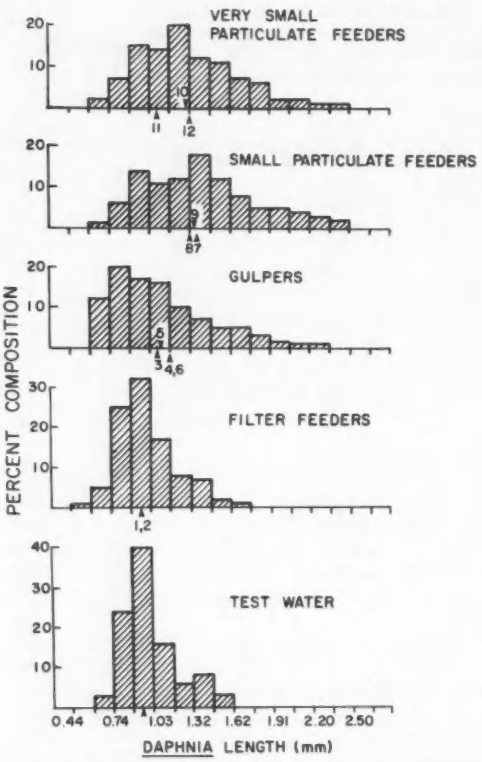

FIG. 1. Prey size distribution in test water and fish of various feeding modes. Arrows denote median prey size for fish; corresponding numbers are the fish numbers in Table 1.

selective feeding. Size distributions of prey eaten by gulpers were not significantly different among themselves, but differed from all particulate feeders except Fish 11, ($P < 0.001$). Distributions of particulate feeders were generally similar but comparisons of a few pairs indicated significant differences. No particulate feeder was significantly different from all others. Thus, the filterers in this study were not size selective; gulpers were size selective; and particulate feeders were more size selective.

About 15,000 prey were consumed, about 3% of the final density. More than half the prey was consumed by filterers (random feeders). Therefore, prey density and size was not altered significantly in this brief experiment.

The total weight of *Daphnia* consumed by filterers was significantly greater than that consumed by other fish (excluding the very small particulate feeders) ($P < 0.05$, $n = 2, 7$ one-tailed Mann-Whitney test, Sokal and Rohlf 1969).

Gulpers consumed 3.1–4.8 prey/s (Table 1). They also gulped at about 2–3 times/s and so, averaged more than 1 prey per gulp. Particulate feeders consumed about 1.9–2.3 prey/s. Filterers consumed 14.5 and 13.6 prey/s.

I have observed only particulate feeding in alewives in the field, but I have observed only small individuals feeding. It would be unlikely that alewives do not filter in nature, otherwise the behavior would not have evolved. The alewife is a native of the Atlantic Ocean, and its filtering may be suited to certain situations found only in marine systems, particularly in highly productive estuaries.

Densities of prey in Lake Michigan are suitable for alewives to filter feed occasionally. Beeton and Barker (1974) found crustacean zooplankton densities of about 29,000–54,000/m^3 in some vertical tows from September to November 1971 and June 1972. Given that zooplankters in Lake Michigan concentrate at certain depths (Wells 1960), certain strata may have densities at or above the 254,000/m^3 in my study. Gannon (1972) found densities of about 250,000/m^3 in Milwaukee Harbor in September 1969, and up to 400,000/m^3 in Green Bay in July 1970. Roth and Stewart (1973) found zooplankton concentrations in excess of 100,000/m^3 in July 1971 and 1972, and 280,000/m^3 in August 1971 in southeastern Lake Michigan.

Filtering could be important at night when prey are less visible. Echosounder tracings indicate that alewife schools disperse at night in Lake Michigan (S. Brandt personal communication and unpublished data) and in the laboratory schools disperse for feeding.

The alewife thus has a nonsize-selective mode of feeding. The importance of this behavior to the fish and to the zooplankton should be a subject of further study.

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Direct and Indirect Effects of Oil on Ringed Seals (*Phoca hispida*) of the Beaufort Sea

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GERACI, J. R., AND T. G. SMITH. 1976. Direct and indirect effects of oil on ringed seals (*Phoca hispida*) of the Beaufort Sea. J. Fish. Res. Board Can. 33: 1976–1984.

Ninety-six ringed seals (*Phoca hispida*) were taken from nets at Brown's Harbour, Northwest Territories in the fall of 1974. Comparison with two other net samples from 1971 and 1972 revealed a lower proportion of young-of-the-year and a lower mean weight of seals in all age-classes. Six seals immersed in Norman Wells crude oil for 24 h at the field netting site suffered only transient eye problems and minor kidney and possibly liver lesions; no permanent damage was observed. Three seals transported to the University of Guelph all died within 71 min after oil was introduced into their pool. Hematologic and blood chemical studies indicate that death was caused by oil superimposed on the stress of captivity. Six, 3–4 wk-old wild whitecoat harp seal (*P. groenlandica*) pups at the Magdalen Islands, Quebec, were coated with crude oil. No significant differences in core body temperatures were noted and no deleterious effects were observed. Five captive ringed seals at Guelph were subjected to a cumulative dosage of Norman Wells crude oil fed with their fish food. High dosage (75 ml) and low dosage (25 ml) of crude oil were also fed to two groups of six harp seal pups. No significant lesions or behavioral changes were noted. These experiments were of an acute nature and reflect the effects of a brief contact with oil only. Effects of longer contact as would probably be the case in an offshore oil well blowout situation are discussed. Possible effects of large-scale offshore oil fields are also considered.

GERACI, J. R., AND T. G. SMITH. 1976. Direct and indirect effects of oil on ringed seals (*Phoca hispida*) of the Beaufort Sea. J. Fish. Res. Board Can. 33: 1976–1984.

On a capturé au filet 96 phoques annelés (*Phoca hispida*) à Brown's Harbour, Territoires du Nord Ouest en automne 1974. Une comparaison avec deux autres échantillons capturés au filet en 1971 et 1972 indique une plus faible proportion de jeunes de l'année et un poids moyen moindre des phoques de toutes classes d'âge. Six phoques immergés dans du pétrole brut de Norman Wells durant 24 h au site de pose des filets sur le terrain ne subirent que des problèmes transitoires d'yeux et des lésions mineures au rein et possiblement au foie; nous n'avons pas observé de dommage permanent. Trois phoques transférés dans les bassins de l'Université de Guelph moururent tous en dedans de 71 mn après introduction de pétrole dans le bassin. Des études hématologiques et chimiques du sang démontrent que la mort est due au pétrole superposé au stress de la captivité. On a appliqué une couche de pétrole brut à six blanchons sauvages de phoque du Groen (*P. groenlandica*), âgés de 3 à 4 semaines, aux îles de la Madeleine, Québec. Nous n'avons pas observé de différences significatives dans les températures du centre du corps et pas d'effets nuisibles. Cinq phoques annelés maintenus en captivité à Guelph reçurent une dose cumulative de pétrole brut de Norman Wells avec leur diète de poissons. Deux groupes de six chiots de phoque du Groenland ont également reçu une dose élevée (75 ml) et basse (25 ml) de pétrole brut. Nous n'avons observé aucune lésion ou changement de comportement significatifs. Ces expériences sont de nature aiguë et réflète les effets seulement d'un bref contact avec le pétrole. Nous analysons les effets d'un contact plus prolongé tel que celui qui résulterait probablement de l'éruption de puits de pétrole au large. Nous examinons également les effets possibles du développement à grande échelle de champs pétrolifères au large.

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THE aboriginal people of the western North American arctic have been dependent on sea mammals since their first occupation of the coastal regions of Alaska over 3000 yr ago (Giddings 1967; Bandi 1969). Because the ringed seal, *Phoca hispida*, is the most abundant marine mammal, and available throughout the year, it soon became the basis of the coastal Inuit economy. Presently, the ringed seal and to a much lesser extent the bearded seal, *Erignathus barbatus*, provide an important source of protein and part of the cash income of most arctic coastal villages. In addition, the ringed seal is the main prey species of the polar bear, *Ursus maritimus* (Stirling and McEwan 1975; Stirling et al. 1975) and one of the essential food items of the arctic fox, *Alopex lagopus*. Both these species in turn provide an important part of the overall cash income of coastal Inuit hunting villages (Usher 1971; Smith 1974).

Recently, the search for petroleum in the Canadian arctic has increased. Oil reserves in the nearshore areas of the southeastern Beaufort Sea have already been proven (Fig. 1). Tentative approval to start drilling in the further offshore areas has been given for the summer of 1976. As the intensity of exploration increases, so does the prospect of major blowouts and oil spills. Our study was designed to evaluate the behavioral, physiological, and pathological consequences of crude oil contact and ingestion on wild ringed seals under field and laboratory conditions. Ten years of data on ringed seal population structure (Smith 1973; Smith et al. 1973) plus stress indicators, (Geraci and Smith 1975; Smith and Geraci 1975) are used to extend the findings to include the probable consequences of large-scale offshore oil exploitation on ringed seal populations.

Materials and Methods

Brown's Harbour, on the east side of Cape Parry, (70°05′30″N, 124°22′30″W) was the site chosen for capturing the ringed seals in August and September 1974. During this period 96 seals, 32 of which were live, were caught by the method described by Smith et al. (1973). All live seals were placed in holding pens measuring 3.6 m^2, constructed of pipe and chain-link fencing. Pens were located in a small saltwater pond near the netting site. Norman Wells (N.W.T.) crude oil was used in the ringed seal oiling experiments. It is not entirely representative of Beaufort Sea oil, but was the only one available for practical use at the time of the study.

Immersion Studies

Prior to immersion in oil, each of six seals was immobilized with ketamine (Geraci 1973), blood samples were taken, and a sonic temperature telemetry pill was administered. Seals were then placed in a pen 2.4 × 2.4 × 1.2 m high that had a plywood floor and sides which allowed water to circulate through a 3-cm opening 35 cm below the oil–water interface. Seals were in the pen for 12 h before oil was introduced. Body temperatures were monitored every 3 h and blood samples were drawn to establish control values. Crude oil, sufficient to create a 1-cm thick surface layer (60 liters), was poured into the pen. Sea ice was then added to cool the water to about 8 C. Seals were left for 24 h, then removed, sampled, examined, photographed, and placed in a clean-water pen. They were monitored continually, and a subsample was killed by gunshot at 2-day intervals and necropsied.

Next, a small group of ringed seals was taken to holding facilities at the University of Guelph, Ontario, where a second immersion study was conducted. There, the effects of low level ingestion of crude oil were also assessed. The oil immersion study at Guelph was carried out in pools 3 × 3.6 × 1.2 m deep, containing water of 24‰ salinity, at about 13 C. The three seals used were apparently in good health and eating Atlantic herring, *Clupea harengus harengus*, and rainbow smelts, *Osmerus mordax*. After 2 mo of acclimation in captivity, they were exposed to oil in the same manner as in the field experiment.

Nine, 3–4-wk-old whitecoat harp seals, *P. groenlandica*, were used to assess the effects of oil coating on temperature regulation in pups. This was done because ringed seal pups were not available for study. The harp seal study was carried out in March 1975 on the Magdalen Islands. Core body temperatures were monitored with the aid of a YSI telethermometer (Yellow Springs Instrument Co., Inc., Yellow Springs, Ohio) fitted with an internal rectal probe. Temperatures were recorded every 4 h for 48 h prior to oiling and continued for up to 4 days after. Six seals were designated as experimentals and three as controls. The experimental seals were well coated by brushing Norman Wells crude oil onto the hair over the entire body. The next day, as a measure of assurance they were recoated in the same manner using crude oil from Mildale, Saskatchewan. Four experimental seals and two controls were killed 3 days after oiling and the remaining ones a day later. All the animals were weighed before and at the end of the experiment. Postmortem examinations were carried out on the dead seals.

Ingestion Studies

Ingestion experiments were carried out to evaluate the effects of seals swallowing a substantial amount of oil during a spill. Seals are not carrion feeders, and any oil which they might consume from live contaminated prey would probably not exceed 5 ml/day. Using this rationale, a low level, cumulative oil-ingestion study was carried out on five ringed seals at Guelph. Blood samples were drawn 6 times during 20 days prior to the experiment. Each seal was then given 5 ml/day of Norman Wells crude oil for 5 consecutive days. Oil was placed in 1-ml capsules and

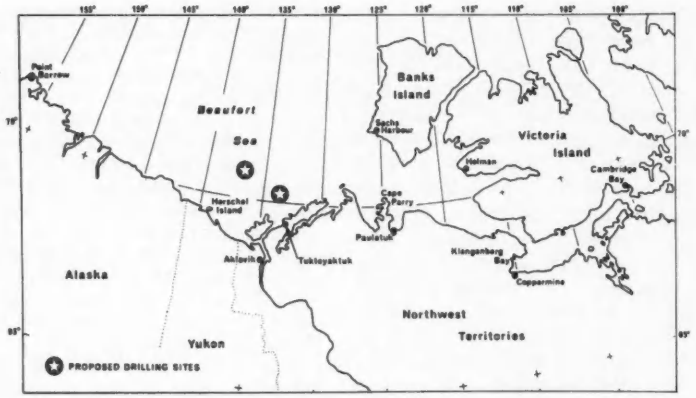

FIG. 1. Proposed Canmar drilling sites in the Beaufort Sea.

inserted into the food fish. Blood samples were taken at frequent intervals for 4 wk after ingestion of oil. Blood was processed for hematology and blood chemistry.

A high level, single-dose ingestion study was carried out on 2–3-wk old fasting harp seal pups. Seals were divided into two groups, each containing six experimental and one control animal. One group was fed 75 ml of Norman Wells crude oil, the other 25 ml, as a single dose. One seal from each group was killed 1, 2, 4, 6, 8, and 10 days after ingestion of the oil. Controls were also killed on the 10th day. Blood samples were drawn from all seals 6–8 h before ingestion of the oil, and again just prior to death.

Analytical Techniques

Blood samples throughout this study were drawn, preserved, and analyzed by the methods described by Geraci (1971), Geraci and Engelhardt (1974), and Geraci and Smith (1975).

Blood was analyzed for plasma chemical constituents by multichannel autoanalyzers, (Technicon Instruments Corp., Ardsley, New York), according to the methodology outlined in Technicon bulletins.

Enzyme activities were determined kinetically and colorimetrically using commercially available kits. Details of the analyses are given in Smith and Geraci (1975).

Results

Description of the Catch

The sex ratio of the catch was 47 males:49 females. The age structure is shown in Fig. 2 and is compared with the age distribution of 208 seals caught in the same location in August and September 1972. The 1974 catch had significantly lower proportions of yearling (0+) seals to older seals (22:61) than the 1972 catch (147:61), ($\chi^2 = 23.2$, $P < 0.005$). A higher proportion of adults, ($\chi^2 = 4.02$, $P < 0.005$) was also seen in the 1974 Brown's Harbour catch compared to the net sample of 124 seals taken in 1971 by Smith et al. (1973) at Herschel Island, Yukon Territory.

Figure 3 shows the mean maximum girth of netted seals from Herschel Island in 1971, Brown's Harbour in 1972 and 1974. The mean girths of yearling (0+) and seals 6 yr and older (adult) were significantly greater in the Herschel seals than those from the Brown's Harbour 1972 or 1974 ($P < 0.005$). Moreover, the 1974 Brown's Harbour yearlings were thinner, and there were more molting animals than in the 1972 sample ($P < 0.005$).

Immersion Studies

In the field experiments the oil formed a uniform film on the surface of the water as soon as it was introduced into the holding pens. For the first 2–3 min, the six animals continued to move about the surface with no apparent recognition of the oil. Because of the swimming movements, the oil quickly became churned into the whole water column, though most of it still remained on the surface. Within 3 min, the heads of the seals were darkened with oil. As they continued to swim about, the hair of the back became oiled, and within 20 min the abdominal hairs became stained.

Seven or eight minutes after the oiling, one of the seals began to lacrimate excessively, and would open and close its eyes. It jumped from the surface and shook its head vigorously. Soon, eye irritation became apparent in the other seals.

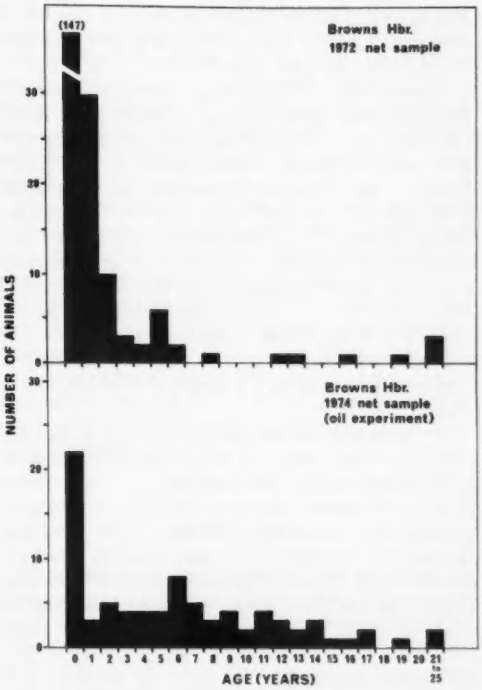

FIG. 2. Age-frequency distributions of seals netted at Brown's Harbour, N.W.T., in 1972 and 1974.

They lacrimated profusely, yet at first there was no attempt to close their eyes and avoid the oil. Twenty minutes into the study, however, some of the seals seemed to have difficulty keeping their eyes open; the conjuctiva of the eyes were obviously reddened and inflamed. Breathing rate of these same seals appeared to increase, and two of them stretched their necks out of the water and shook their heads. The animals were also observed to force air through their nostrils making an audible sound when at the surface. This general behavior seemed to persist throughout the first 4 h by which time all of the seals were lacrimating and squinting.

Throughout the remaining exposure period, five of the seals remained submerged most of the time, the sixth and most aggressive of the group would remain on the surface and continue its agonistic behavior towards approaching persons or other seals. When on the surface all of the seals showed varying degrees of arching of the back, a behavior that was not observed in the control group nor in the experimental group prior to oiling.

Twenty-four hours after the introduction of the oil, the seals were removed from the pen and

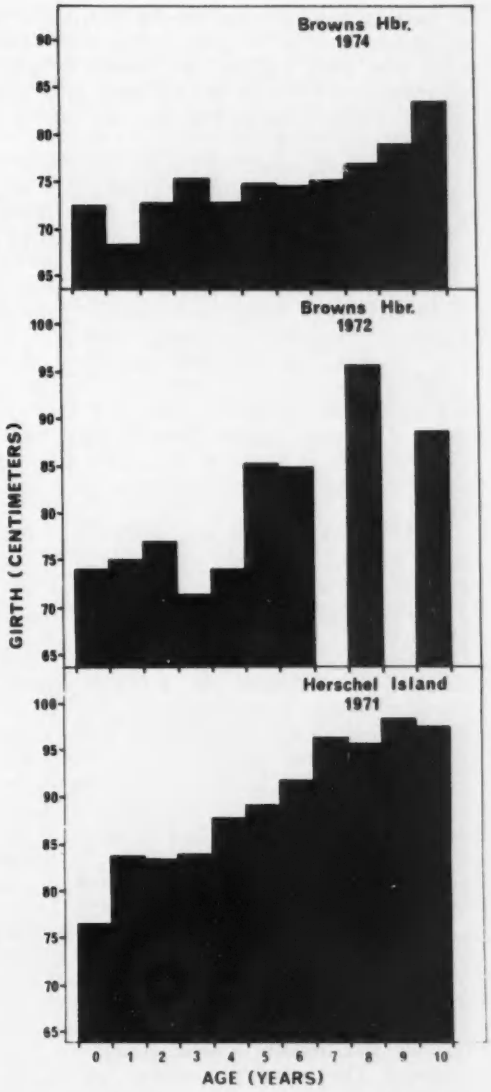

FIG. 3. Girth per age-class of seals netted at Brown's Harbour, N.W.T., in 1972 and 1974 and at Herschel Island, Y.T. in 1971.

examined. All showed obvious signs of eye disturbances, characterized by blinking, squinting, lacrimation, and severe conjunctivitis with swollen nictitating membranes; some evidence of corneal erosions and ulcers were also noted.

Within 3 h of being placed into a clean-water holding pen most of the eye squinting subsided, there was less lacrimation, the seals remained quiet and calm, and body quivering and arching

of the back was no longer detectable. After 20 h all appeared to be in good health. Their hair coats were clean and the eyes showed no signs of irritation. By the 3rd and 4th days, there was scarcely visible evidence that the seals had been contaminated by oil.

Temperatures, which were monitored throughout the oil-exposure study, remained stable with a mean core temperature of 37.7 C (SD = 0.66).

Hematologic and plasma chemical analyses taken throughout the oil immersion study revealed few consistent patterns of change. Plasma levels of calcium, blood urea nitrogen, glucose, cholesterol, bilirubin, potassium, chloride, protein, albumin, and inorganic phosphorus were unaffected by exposure. There were significant but inconsistent changes in uric acid levels in three of the seals. Sodium levels dropped below 147 mEq/liter in 4 out of 20 samplings in six seals, twice before oiling, and twice 24 h after oiling.

Eight plasma enzymes were analyzed. In four seals, glutamic oxalacetic transaminase, an enzyme of muscle and liver origin, decreased from abnormally high levels at the beginning of the experiment, to normal values at the end. In the two remaining seals, the pattern was reversed. Creatine phosphokinase, also a muscle enzyme, decreased in five out of the six seals. The remaining enzymes alkaline phosphatase, lactic dehydrogenase, glutamic pyruvic transaminase, sorbitol dehydrogenase, gamma-glutamyl transferase, and leucine amino peptidase remained within normal limits throughout the experiment, as did all of the blood cellular elements. Individual values for all the parameters considered are detailed in Smith and Geraci (1975, tables 5–10).

Three seals were used in a laboratory immersion study. Norman Wells crude oil was poured into the holding tank and came into contact with the seals within 2 min. Almost immediately, all three animals began to shake vigorously. Eye blinking and frequent audible exhalations were observed. This behavior continued for 15 min during which time the seals remained underwater for unusually long periods. Twenty minutes after the oiling, a haul-out platform was provided. The seals made no attempt to climb onto it. Swimming movements were uncoordinated. One animal made determined attempts to leave the pool, thrashed on the surface along the edge, dived, and died 21 min after oiling.

Twenty minutes after the oil was introduced, the two remaining seals stopped thrashing and became quiet on the surface of the pool, but milder trembling and forced exhalation continued. The second seal died 60 min after the oiling. The behavior of the last seal remained essentially unchanged until it thrashed about briefly and died 71 min after contact with the oil.

Hematologic and plasma chemical studies performed before oiling and immediately after death revealed significant differences in six parameters. Uric acid increased from a range of 2.8–4.2 to 5.4–5.7 mg/100 ml. Hydrocortisone decreased from 80–150 to 55–70 μg/100 ml. Potassium, increased from 3.6–4.1 to 6.6–7.8 mEq/liter. The white blood cell count and the total eosinophil count remained unchanged in the seal that died after only 21 min of exposure, whereas the two remaining seals showed marked total white cell reductions of from 50 to 75%, and eosinophil counts decreased to 15–33% of the pre-oiling values.

In the field oil-coating study conducted on harp seal pups there were no significant differences in core temperatures between pre- and post-oiled seals or between the experimental and control groups. No behavioral changes were observed during the experiment. All seals showed a weight loss through the study period during which time they were not fed. There were no pathological changes which could be attributed to oil coating.

Ingestion Studies

There were no obvious deleterious effects or behavioral alterations in any of the experimental animals throughout the study. Of all the blood parameters analyzed, only creatine phosphokinase showed changes. Three of the four animals had appreciably higher levels after ingestion.

When oil was fed in a single high dose to harp seal pups in the Magdalen Islands, its presence was noted on the anus and on the hind flippers 1½ h later. This occurred in the low dose (25 ml) and high dose (75 ml) groups. Most of the oiled seals fell asleep within 6–8 h after ingestion, at which time the controls had already been asleep for 4 h. Ten hours after oiling, one highly dosed animal appeared to be unusually unresponsive to manipulation. This behavior was not apparent on subsequent observations. For 12 h from the time oil excretion was first noted, the pelts were stained yellow from rolling in oil-covered snow. When they were moved to clean snow, the pelts became almost white again within 24 h. Aside from these findings, all observations made hourly up to 24 h after ingestion of oil, and at 3 h intervals thereafter, revealed no significant differences in behavior or health between the control and experimental seals.

During the high dose study, plasma levels of muscle-based enzymes, CPK, GPT, and aldolase showed a definite and significant pattern of de-

cline from the beginning to the end of the experiment. This pattern occurred in the high and low dose groups as well as the controls. Individual values are shown in Smith and Geraci (1975, tables 18 through 25). Sorbital dehydrogenase showed a single peak of high activity 48 h after high-dose administration, reflecting transient liver damage.

Significant hematologic findings were confined to packed cell volume which increased with time in control as well as experimental animals. The increases, which reflect hemoconcentration or dehydration, were in the order of 0.5–50.6% within the 10-day experimental period. This finding was consistent with the 5.7–24.5% weight loss in all the animals during the experimental period and reflects the fact that they were not fed during the study. Necropsy on the seals did not reveal significant lesions.

Discussion

The present study shows that up to 75 ml of ingested crude oil is not irreversibly harmful to seals. The liver is generally regarded as a prime target organ for hydrocarbon damage in mammals. Effects of such damage have been well documented (Cornelius and Kaneko 1963). If sufficient quantities of these hepatotoxic substances are administered, liver enzymes are released into plasma and are detectable. Degree and duration of enzyme release is generally a function of the quantity and toxicity of the substance(s). Geraci (1972a) induced measurable liver damage in gray seals, *Halichoerus grypus*, using 5 and 10 ml of carbon tetrachloride, a rather potent fraction. In the present studies, there was only transient liver enzyme release. If there was liver damage, it was negligible. The release and subsequent decline of muscle-based enzymes during the study reflect the vigorous capture handling activity which was imposed on the seals: it was transient and not related to oil. Similarly unrelated was the observed weight loss and hemoconcentration which are physiologically natural events associated with postweened fasting whitecoat pups.

Surface contact with oil had a far greater impact on the seals than did absorption. Such direct effects of oil can be categorized as physical, physiological, and behavioral. The simple physical fouling of birds and fur bearing mammals has been well documented (Hartung 1967). The picture in marine mammals is not clear. Literature does exist indicating that seal deaths have been associated with Bunker C fuel oil (Warner 1969; Anon 1970). However, the reports do not convincingly indicate that the observed mortality was directly linked to contact with oil. Postmortems were not performed and data were not provided for comparison of the natural mortalities in years when no oil spills occurred. Other reports indicate that although large numbers of seals had come into contact with oil, no mortalities were observed (Hess and Trobaugh 1970; Morris 1970; Muller-Willie 1974). Some evidence also exists that gray seals actively avoid oil slicks (Anon 1970). LeBoeuf (1971) and Brownell and LeBoeuf (1971) in reliable investigations of the crude oil spillage in the Santa Barbara Channel observed no deaths of seals that could be related to oil. In spite of this, popular press and scientific review papers (Nelson-Smith 1970) referring to the incident strongly imply that seal deaths were actually caused by the oil.

In the present study, oil fouling with Norman Wells crude oil did not cause any mechanical damage such as sticking of the flippers to the body or the plugging of body openings. It should be pointed out that Norman Wells crude oil, which is similar to Beaufort Sea oil, is relatively light, highly volatile, and of low viscosity. It is unlikely that such an oil can be compared to the more viscous crudes and to fractional products such as Bunker C, in its physical fouling characteristics.

Hair in postweaned phocid seals contributes little to their overall insulation (Irving and Hart 1957); no thermoregulatory problems were expected and none were observed. Core body temperatures of oiled seals showed no trends indicating increased thermal conductivity such as occurs in other fur-bearing mammals (McEwan et al. 1974). This was also true in the oil-coating studies on whitecoat harp seals which were between 2 and 4 wk old, even though Øritsland and Ronald (1973) showed that the white lanugo does provide protection against skin cooling by the wind. It may be significant that the pups in the present study had already developed blubber layers of between 2.5 and 5.0 cm, which apparently was enough to prevent surface heat loss. Seals between the time of birth and the laying down of the blubber are more dependent on hair for insulation and, presumably, would be vulnerable to the thermal effects of oil coating. In the event of an under-ice oil spill the ringed seal pups, which are born in early April and occupy subnivean birth lairs (Smith and Stirling 1975), could be exposed to an oil-fouled ice surface and a layer of oil at the water–ice interface for the whole of the suckling period. It is unlikely that the adult female seal would be able to move the pup away from the contaminated area until it had been weaned.

Eye damage was a significant finding in the field oil study. At least some of the damage appears to have been done by volatile components of the oil. Nearly all of the investigators experienced eye irritation when exposed to the pungent fumes in the seal pen. The eye inflammations in the seals subsided soon after they were placed in clean water. Continued exposure to oil may have resulted in more severe and possibly permanent eye disorders. Nelson-Smith (1970), quoting an unidentified source, states that oil damage in seals frequently includes severe eye irritation, and makes reference to a female seal, now blind, which was rescued during an oil spill. Eye damage and blindness are observed in wild and captive seals (King 1964; Ridgway 1972), and the occurrence in nature need not be linked with oil or other noxious substances. Nevertheless, oil is irritating and damaging to eyes and the severity of damage is likely to be related to exposure time and to the concentration of volatile components.

Divergent results were obtained from the ringed seal field and laboratory immersion studies. Apart from eye damage and behavioral changes, at least one seal in the field study showed some histologic evidence of kidney damage. The lesions may be related to an attempt to concentrate and/or excrete oil or its metabolites via the urinary system. This route has been confirmed by F. R. Engelhardt (Southeastern Massachusetts University, personal communication), who observed the presence of high kidney and urine oil concentrations which persisted at decreasingly lower levels for 6 days after immersion. The ultimate consequences of the kidney lesions can be assessed only with a long-term study.

Seals in the Guelph immersion study provide a clue to an important factor which could complicate the effects of an oil spill. They responded to oil with nearly convulsive behavior and died in just over an hour. These findings point to stress, with death triggered only by the presence of oil. Stress is a rather common condition of phocid seals. Generally, it has been regarded as a disease of captivity. The exact mechanism is unknown, but it is probably related to adrenal insufficiency (Geraci 1972b). Affected animals become uncoordinated, display muscle quivering, and have electrolyte disturbances. When further stressed in any way, they often die with little or no warning (Geraci 1972a, b). The Guelph study adds oil to the growing list of factors that can trigger the death of stressed seals.

Recently, we have shown that stress also occurs and can be assessed hematologically in wild ringed seals (Geraci and Smith 1975). The electrolyte disturbances, which characterize the condition, have been found in emaciated and late molting animals (J. R. Geraci and T. G. Smith unpublished data). Assuming that animals so stressed respond as do captive stressed seals, then any severe disturbances, including contact with oil, would conceivably have a selective effect on the populations, eliminating those animals in poor condition. Typically, this would include isolated seals that are diseased and heavily parasitized.

The large areas of open water in the Beaufort Sea shear zone are important to the adolescent nonbreeding population as easily maintained breathing spaces and probably as areas of maximum winter food concentration. In a winter such as was seen in 1974 these leads were not open much of the time because of a lack of prevailing northwest winds. A heavy concentration of shifting, broken ice persisted throughout the summer of 1974 along the mainland coast of the eastern Beaufort Sea and southern Amundsen Gulf. In more typical years the ice disappears completely from these areas during mid-July to early October. The 1974 and 1975 net catches at Brown's Harbour differed from catches there in 1972 and at Herschel Island in 1971. All animals in the 1974 and 1975 catches were in poorer physical condition as seen by their lower average weight and extended molting period. There was also a significantly lower number of pups, possibly indicating that the generally poor feeding conditions also affected the annual production of young. During years such as these, the effects of an environmental disturbance would presumably be more widespread, affecting entire age-classes and weakened segments within the population.

Other factors related to the life history of ringed seals bear on the ultimate consequences of a spill. Seals in the Beaufort Sea and Amundsen Gulf appear to depend on the vast offshore and inshore areas. The largest harvest is taken at Holman in the Amundsen Gulf. Preliminary calculations based on population estimates and reproductive rates indicate that the Holman harvest depends on a larger area than the Amundsen Gulf for its sustenance. Direct tagging evidence shows movement of seals between the Beaufort Sea and Amundsen Gulf to a point as far west as Point Barrow and the eastern Siberian coast. Thus, a spill in a given area such as from the proposed Canmar drill sites (Fig. 1) could affect the harvest in areas as far east as Holman or as far west as the hunting villages along the Alaskan north slope.

In conclusion, offshore oil exploitation can adversely affect the ringed seal population of the

Beaufort Sea. The direct effects of an oil blowout or spill, to which healthy seals are briefly exposed may cause transient though severe eye damage. Such brief exposure can occur only during the open water season from July to October when seals are free to move out of a contaminated area. Prolonged contact during the remaining months of fast ice will likely result in permanent eye disorders. Preweaned seals 2 mo old and under inhabiting subnivean birth lairs (Smith and Stirling 1975) will be more susceptible to the thermal effects of oil than postweaned seals, which rely on blubber rather than hair for insulation. Consequently, oil fouling during the birthing and nursing months of April–June may have a more serious effect on that age-class, especially if the spill occurs in a region of high seal production. Adverse environmental conditions which result in low food production may further complicate the effects of oil by selectively affecting the stressed seals in poor nutritional condition.

Because of the relatively low productivity of the Beaufort Sea (Grainger 1975; Wacasey 1975) and consequently large areas needed to maintain the present ringed seal population, no simple recommendations can be made to minimize the possible adverse effects of petroleum related activities. Certainly, any model attempting to predict the consequences of oil fouling must take into account the season of spill, the productivity of the area, and the variable health status of the population. In the Beaufort Sea the mere presence of a large offshore oil field of the type already in existence in the North Sea may well effect the seasonal pattern of movement of seals. This could have serious consequences in reducing the ability of these mobile populations to survive adverse natural conditions. It might also seriously reduce the catch of seals in some of the important hunting communities.

Acknowledgments

We thank Dr R. Thomson, and Messrs D. St. Aubin, T. Austin, A. Gilman of the Pathology Department, University of Guelph, and Dr F. R. Englehardt, Southeastern Massachusetts University. Hahgagiak of Holman, Northwest Territories, assisted in the field studies. We wish to thank the Polar Continental Shelf Project for logistic support, Mr J. Holer, Niagara Marineland and Game Farm for providing maintenance facilities for some of the seals, and Dr J. Schroder and Mr J. Parsons for seal maintenance at Guelph.

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Pollution Symposium — 13th Pacific Science Congress

Sublethal Effects of Pollution on Aquatic Organisms

Contents

Preface/Préface	**M. Waldichuk**	1986–1987
Current status of sublethal tests of pollutants on aquatic organisms	**J. B. Sprague**	1988–1992
Fish tumors and sublethal effects of pollutants	**H. F. Stich, A. B. Acton, and C. R. Forrester**	1993–2001
Reentry of 5-year-old stranded Bunker C fuel oil from a low-energy beach into the water, sediments, and biota of Chedabucto Bay, Nova Scotia	**J. H. Vandermeulen and D. C. Gordon Jr.**	2002–2010
Epidermal papillomas of flatfish in the coastal waters of Hokkaido, Japan	**K. Oishi, F. Yamazaki, and T. Harada**	2011–2017
Effects of polluting substances on enzymes of aquatic organisms	**G. W. Brown**	2018–2022
Effects of copper on downstream migration, gill ATPase, and adaptation to sea water of juvenile coho salmon (*Oncorhynchus kisutch*)	**H. W. Lorz and B. P. McPherson**	2023–2030
Progress in sublethal effect studies with kraft pulpmill effluent and salmonids	**J. C. Davis**	2031–2035
Effects of sublethal concentrations of pollutants on the behavior of fish	**H. Kleerekoper**	2036–2039
Monitoring procedures for chemical carcinogens in coastal waters	**B. P. Dunn and H. F. Stich**	2040–2046
Sublethal effects of environmental stressors, natural and pollutional, on marine fish eggs and larvae	**H. Rosenthal and D. F. Alderdice**	2047–2065

Preface

When I was asked to organize a session on water pollution in the "Aquatic Resources and their Management" symposium of the 13th Pacific Science Congress, held in Vancouver, B.C., August 18–30, 1975, I attempted to focus on a subject that had both relevance to the central theme of the Congress, "Mankind's Future in the Pacific," and was topical in interest. We had heard a great deal about pollution in various aspects of the human environment during the past decade. Water pollution had manifested itself in many ways — fish kills, soiled beaches, closed shellfish areas, banned fishing, posted bathing areas, and algae-ridden lakes. We could probably have had a series of further reports on such incidents and added to our inventory of information on pollution observations.

However, it dawned on me that we should be looking at ways of detecting the onset of pollution before the clearly overt symptoms appear. We should be seeking an early warning system. Once dead fish have appeared, it may be too late to take pollution control measures without enormous expenditures. There is always the haunting concern that we are making changes in our environment that will be noted only years hence. It has been said that we may be slowly titrating our aquatic systems to an end-point represented by catastrophe, e.g. inhibition of methyl transfer processes, such as occur in fermentation, through reactions with vitamin B_{12}.

Therefore, we decided that we should look at the more subtle and insidious effects of water pollution. We chose the title of "Sublethal Effects of Pollution on Aquatic Organisms." We invited four speakers who are authorities in their fields to review the state of knowledge in their areas of expertise: Dr J. B. Sprague on acute and sublethal bioassays; Dr H. Kleerekoper on sublethal effects of pollutants on behavior of fish; Dr H. F. Stich on sublethal effects of pollutants and cancer in fish; and Dr D. F. Alderdice on the sublethal effects of pollutants on fish eggs and larvae. Other scientists were invited to contribute papers that have relevance to the subject of sublethal effects.

It was considered useful to publish the invited papers along with a selection of contributed papers in one place to make them available to workers in this important field. I am grateful to the Editor of the *Journal of the Fisheries Research Board of Canada* for making this possible. I should like to extend my thanks also to Dr W. S. Hoar, Secretary-General of the 13th Pacific Science Congress, and to Dr N. J. Wilimovsky, organizer of the Symposium on Aquatic Resources and their Management, for their encouragement and assistance in processing enquiries and abstracts for the Congress program. Finally, I wish to acknowledge the willing assistance provided by Dr J. C. Davis in arranging and organizing the program on sublethal effects for the Congress.

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Préface

Lorsqu'on m'a demandé d'organiser une séance sur la pollution de l'eau dans les cadres du colloque « Ressources aquatiques et leur gestion » du 13e Congrès des sciences du Pacifique, tenu à Vancouver, C.-B., du 18 au 30 août 1975, j'ai voulu concentrer mes efforts sur un sujet qui était à la fois pertinent au thème central du congrès, « L'avenir de l'homme dans le Pacifique », et également d'actualité. On a beaucoup parlé au cours de la dernière décennie de pollution dans divers domaines de l'environnement humain. La pollution de l'eau s'est manifestée de bien des façons — mortalités massives de poissons, plages souillées, zones fermées à la récolte des mollusques, pêche interdite, aires de natation limitées et lacs étouffés par les algues. On aurait probablement pu présenter une série de rapports supplémentaires sur de tels incidents et grossir notre inventaire d'observations sur la pollution.

Cependant, il me vint à l'idée que nous devrions plutôt examiner les moyens de détecter le début des pollutions avant que les symptômes n'apparaissent. Nous devrions chercher un système avancé de pré-alerte. Quand apparaissent les poissons morts, il est peut-être trop tard pour appliquer des mesures de contrôle de pollution sans qu'il en coûte des sommes considérables. Nous soumettons l'environnement à des changements qui ne se feront sentir que plusieurs années à venir, et c'est là un sujet constant d'inquiétude. Quelqu'un a affirmé qu'on était en voie de titrer lentement nos systèmes aquatiques vers un point de virage représenté par la catastrophe, e.g. l'inhibition des processus de transfert du méthyl, comme cela se produit dans la fermentation, par le biais de réactions avec la vitamine B_{12}.

Nous avons donc décidé qu'il nous fallait considérer les effets plus subtils et insidieux de la pollution de l'eau. Nous avons adopté comme titre « Effets sublétaux de la pollution sur les organismes aquatiques ». Quatre orateurs, des autorités dans leur domaine respectif, ont été invités à passer en revue l'état des connaissances dans les domaines de leur compétence: M. J. B. Sprague sur les essais biologiques aigus et sublétaux; M. H. Kleerkoper sur les effets sublétaux des polluants sur le comportement des poissons; M. H. F. Stich sur les effets sublétaux des polluants et cancer chez les poissons; et M. D. F. Alderdice sur les effets sublétaux des polluants sur les œufs et les larves de poissons. D'autres scientifiques ont été invités à soumettre des travaux se rapportant aux effets sublétaux.

Nous avons jugé bon de publier au même endroit les articles préparés sur invitation et des contributions choisies afin de les rendre accessibles aux chercheurs dans cet important domaine. Je dois remercier le directeur de la publication du *Journal de l'Office des recherches sur les pêcheries du Canada* pour avoir rendu la chose possible. Je voudrais également remercier M. W. S. Hoar, secrétaire général du 13e Congrès des sciences du Pacifique, de même que M. N. J. Wilimovsky, organisateur du colloque sur Les ressources aquatiques et leur gestion, pour leur encouragement et leur aide dans le traitement des demandes de renseignements et des résumés pour le programme du congrès. Je désire enfin remercier M. J. C. Davis, qui a bien voulu nous aider à agencer et à organiser le programme sur les effets sublétaux.

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Current Status of Sublethal Tests of Pollutants on Aquatic Organisms[1]

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SPRAGUE, J. B. 1976. Current status of sublethal tests of pollutants on aquatic organisms. J. Fish. Res. Board Can. 33: 1988–1992.

In the U.S. government's book *Water Quality Criteria, 1972*, 75 recommendations for "safe" levels of toxic pollutants were found in the sections on freshwater and marine aquatic life. Ten recommendations gave no specific numerical value, 20 seemed arbitrary, and a further 10 were essentially lethal concentrations. Thus, 40 of the 75 recommendations are somewhat unsatisfactory, mostly because adequate scientific basis is not yet available.

For the other 35 recommendations based on sublethal or chronic effects, most (13) were derived from tests on reproduction and young stages of aquatic organisms. All other categories of physiological tests yielded only 10 criteria. Tissue residues were the basis for 7 recommendations but some were arbitrarily derived from tolerance levels in human food. Field observations gave rise to 5 criteria.

Experiments on reproduction of organisms seem the most productive for useful results. Such tests with small tropical fish would be much more economical than those with longer-cycle fish native to the north. *Daphnia* and algae yield high proportions of useful data and are even faster. Investigations of blood parameters, enzyme systems, etc., are more suitable for unravelling mechanisms of effect, but significance of pollutant effects is best determined at higher levels of integration. Responses such as avoidance may have been understudied, and may be more sensitive for some pollutants. Field experiments should receive more emphasis, as a final test of laboratory predictions. Studies of tissue residues should include biological effects, if any, not merely measurements of levels present.

SPRAGUE, J. B. 1976. Current status of sublethal tests of pollutants on aquatic organisms. J. Fish. Res. Board Can. 33: 1988–1992.

Dans l'ouvrage américain *Water Quality Criteria, 1972*, on trouve, aux sections sur la vie aquatique en eau douce et en mer, 75 recommandations concernant les niveau «sûrs» de polluants toxiques. Dix recommandations ne mentionnent pas de valeurs numériques spécifiques, 20 semblent arbitraires et 10 sont essentiellement des concentrations létales. Sur un total de 75 recommandations, 40 sont donc plus ou moins satisfaisantes, surtout à cause du manque de fondement scientifique.

Quant aux 35 autres recommandations basées sur les effets sublétaux ou chroniques, la plupart (13) résultent d'essais sur la reproduction et sur les jeunes stades d'organismes aquatiques. Toutes les autres catégories d'essais physiologiques ne donnent que 10 critères. Les résidus tissulaires ont servi de base à 7 recommandations, dont quelques-unes cependant ont été déduites des niveaux de tolérance dans les aliments humains. Des observations sur le terrain ont fourni 5 critères.

Les expériences sur la reproduction d'organismes, semble-t-il, sont celles qui produisent le plus de résultats utiles. De telles expériences, effectuées sur de petits poissons tropicaux, seraient beaucoup plus économiques que celles effectuées sur des poissons natifs du nord dont le cycle biologique est plus long. Les daphnies et les algues fournissent beaucoup de données utiles et sont même encore plus rapides. Les recherches sur les paramètres sanguins, les systèmes enzymiques, etc., conviennent mieux au démêlement des mécanismes d'effets, mais c'est à des paliers d'intégration plus élevés qu'on peut le mieux déterminer la signification des effets des polluants. Il est possible qu'on n'ait pas suffisamment étudié les réactions, comme celles de l'évitement, qui peuvent être plus sensibles dans le cas de certains polluants. On devrait attacher plus d'importance aux expériences sur le terrain, comme test final de prédictions obtenues en laboratoire. Les études sur les résidus tissulaires devraient inclure les effets biologiques, lorsque présents, et non pas seulement les mesures des niveaux présents.

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THIS will be a practical and applied look at testing sublethal effects of pollutants on aquatic organisms. Today, a strong reason for doing such tests is to produce hard numbers on "safe" concentrations. Until the mid-1950s, biologists were reluctant to state such numbers, much to the frustration of engineers who designed waste-treatment systems. Now it is generally realized that without such numerical goals based on biology, there can be no rational strategy for water pollution control. Indeed, we now see laboratories full of biologists churning out experiments on how pollutants affect fish.

The best current tabulation of numbers resulting from such work is the U.S. government's "blue book" *Water Quality Criteria 1972* (National Academy of Sciences/National Academy of Engineering 1974), finally released in late 1974. It seems opportune to examine the criteria in the book and describe our state of progress. The purpose of this paper is to see how many hard numbers we have for aquatic organisms, and what methods were most productive in yielding them.

Materials and Methods

To do this review, I examined two sections of the blue book, those dealing with criteria for freshwater and marine aquatic life. These sections represent the efforts of two panels of 63 professionals, toiling during about 1½ yr. I found 75 recommendations dealing with harmful materials or conditions, excluding a few such as mixed and deoxygenating wastes. For each recommendation, I went through the supporting text and tried to determine which experimental result was the key one in recommending the criterion. I tabulated these under various categories as will be evident. In some cases, the criterion seemed to be based on two, three, or more results which yielded similar answers. In these cases, I credited the different categories with fractions of unity, so results will not necessarily be whole numbers.

The procedure is fraught with inaccuracies. Different people would probably use different categories or arrive at somewhat different proportions in the categories. In many cases, I apparently did not have the same crystal ball available as did the learned panelists. Of course, the panels could only work with available information. Thus, the most sensitive and productive experimental procedures may be poorly represented because few people had worked with such methods.

Results and Discussion

The overall pattern of results is somewhat surprising. In 30 of 75 recommendations, category A in Table 1, there were no numerical criteria, or else firm scientific bases for the numbers were not obvious in the accompanying text. In almost 10 more cases, category B, the criteria were merely lethal levels of the pollutant, albeit sometimes levels that just failed to be lethal upon long exposures such as 30 days. Obviously it is not very satisfactory to recommend criteria which may eventually result in dead fish. Today's objective must be levels that will not cause sublethal effects. Accordingly, I consider that the first two categories (i.e. about 40 out of 75 recommendations) represent an inadequate state of scientific knowledge; i.e. not enough information on sublethal effects was available to the panelists.

Looking at categories A and B in greater detail, we see that 10 of the recommendations had no numerical value. A further 20 recommendations had one kind or another of arbitrary value. Of course these numbers might be based on reasonable personal knowledge of the panelists, but this was not documented in the text. "Application factors" are mentioned in A; these are merely numbers such as 0.1, used as a multiplier of a lethal concentration, to arrive at a predicted "safe" concentration for sublethal effects. I called them arbitrary in A, because there was no internal evidence that the selected application factors were correct for those particular pollutants.

Looking at criteria based simply on lethal levels, category B, about 7 of the 10 cases are for fish and 2.5 for invertebrates. Or from another point of view, 7 of the 10 are based on acute tests, usually lasting 4 days, and less than 3 cases are for longer exposures.

The 35 criteria based on sublethal or chronic data comprise only 47% of the total. The largest category is C, for work on reproduction, reproductive products and young stages. These are split about equally between fish, and invertebrates plus algae. One third of this category was based on chronic reproductive studies with *Daphnia* and *Gammarus*, chiefly the former.

Category D is the second largest group among sublethal effects and covers all other kinds of physiological and histological work. Within D, the largest unit of 3 cases is not as revealing as it might seem, since it is really a catchall for conclusions based on massive reviews of the literature. The next largest unit is for work on algae. The importance of this item looms larger since relatively fewer investigators are working in this field. One might think that the other six topics listed in D would be productive of useful results, but they have not yielded them.

Category E on tissue residues produced a fairly large number of criteria, more than 7 or 10% of all recommendations. However, information on

TABLE 1. Tabulation of the apparent bases for recommendations given in the sections on freshwater and marine aquatic life of U.S. government's *Water Quality Criteria 1972* (National Academy of Sciences/National Academy of Engineering 1974). If there were more than one experimental basis for a recommendation, fractional values were assigned. Numbers may not add exactly because of rounding. (a.f. = application factor.)

A. No clear basis			
No specific numerical value		10	
Arbitrary level alone, or arbitrary a.f. alone		8.5	30
Arbitrary a.f. with lab. lethal level: fish	10.5	11.5	
invertebrates	1		
B. Laboratory lethal levels alone			
Fish: acute tests	5.7	7.3	9.8
subacute or long-term	1.7		
Invertebrates: acute	1.5	2.5	
subacute or long-term.	1		
Subtotal of categories A, B			39.8
C. Reproduction, eggs, larval tests			
Fish: chronic reproduction in lab.	2.7		
egg and larval development	3.3	7	
field observation on spawning requirements	1		
Invertebrates: chronic reproduction, *Daphnia*, *Gammarus*	4.3		13
egg and larval development	0.7	6	
Algae: populations developed in lab.	1		
D. Laboratory physiological tests			
Fish: general review or variety of physiology, histology	3		
swimming performance	1.2		
growth, food conversion	1	6.7	
avoidance	0.5		
respiration	0.5		10
sensory perception	0.5		
Invertebrates: oyster pumping rate	0.5		
Algae: photosynthesis or growth in lab.	2.8		
E. Tissue residues			
Found to affect aquatic organisms	1.5		
Affecting bird reproduction through food chain	2.5		7.3
Tolerances for human food, or arbitrary and apparently based on those values.	3.3		
F. Field observations			
Fish and birds	2.8		4.8
Production of plants	2		
Subtotal of categories C, D, E, F.			35.1
TOTAL			75

residues may have been given added emphasis in the blue book because of recent scares concerning cumulative toxicants. Three of the seven cases are really based on tolerance levels for human food and do not seem to be related by any direct evidence to effects on aquatic organisms. Since the tolerance levels for human food are in themselves sometimes rather arbitrary, category E might have been reduced in importance by relegating these 3 cases to the "no clear basis" of category A.

The lowest number of criteria were based on field observations, category F. This reflects several difficulties in field work: assessing fluctuating concentrations of a pollutant in natural systems, assessing the usual situation of mixed pollutants, getting accurate measurements on wild populations, and the frequent absence of an unpolluted baseline condition for comparison. Nevertheless, we must consider that field observations are the final tests of laboratory prediction. As knowledge accumulates and techniques are refined, field experiments should undoubtedly receive more emphasis.

Conclusions

The first obvious conclusion is that we are still far from achieving a good experimental basis for water quality criteria for aquatic life. The panel-

ists had information on sublethal effects for less than half of the blue book recommendations.

A second conclusion is that the most sensitive and productive experiments seem to be chronic ones on reproductive cycles or young stages of organisms. Reproductive experiments on invertebrates, especially crustaceans, seem to be particularly useful considering the smaller proportion of work being done on these compared with that on fish. Furthermore, experiments with the crustacean *Daphnia* are economical since this animal reproduces in a few days. Similarly, algae seem to be sensitive test-organisms, using either population levels or photosynthetic production. These could be even faster than tests with *Daphnia*. However, the investigator must have achieved a careful mastery of the art and science of culturing either *Daphnia* or an alga.

Applying the same rationale to reproductive tests with fish, it would seem reasonable to use species which come to maturity rapidly. Examples would be the flagfish (*Jordanella floridae*) and the zebra fish (*Brachydanio rerio*). These would allow a one-generation experiment in 3 mo. Either species is amenable to laboratory conditions and would be much more economical than the commonly used native northern American species, the fathead minnow (*Pimephales promelas*) and the brook trout (*Salvelinus fontinalis*). They take 1–2 yr for a life-cycle experiment. The guppy (*Poecilia reticulata*) might seem a logical choice, but apparently it is relatively resistant to toxicants. More work is needed to determine if the other two tropical fish are reasonably equal in sensitivity to native fish of other regions.

A third general conclusion concerns the physiological tests in category D. These have yielded disappointingly few criteria considering the large number of scientific investigations in this field. Possibly this is because there is more interest in unravelling the intricacies of a particular physiological discipline, than in providing water quality criteria. Growth experiments might be taken as an example of a technique which has not proved sensitive nor provided many criteria. This is surprising, since growth experiments might be expected to reflect overall integration of damage to an organism and be on an equal footing with reproductive tests. Yet this and all other physiological tests in category D put together have yielded fewer criteria than tests on reproduction and young stages. This general conclusion may be exemplified by the work of McKim et al. (1970). Effects of copper on five blood parameters were either transient with reference to 1-yr exposures, or less sensitive than effects on reproduction, growth, and survival.

Notably absent as major categories are experiments at the tissue level of organization, or at lower levels, for example blood parameters, enzyme systems, and electron microscopy. Apparently the role of such studies is to explain the mechanism of deleterious effect, after the significance of an effect has been demonstrated at the level of the whole individual, the population, or the ecosystem.

A fourth conclusion is that there may be several underrated procedures, as mentioned previously. One such possibility is avoidance reactions. For example, rainbow trout (*Salmo gairdneri*) in the laboratory avoided zinc at about the same concentrations as those which affected reproduction of fathead minnows (Brungs 1969; Sprague 1968). The reproductive effect was the one used as the basis for the blue book criterion, and it was at an unusually low level compared to the lethal concentration (application factor = 0.005). Even more pointed are the results of a field experiment by the U.S. Environmental Protection Agency in Schayler Run, a stream in Ohio (Geckler 1976). In that controlled field experiment, reproduction was affected by copper at the same concentrations found in laboratory work. The field reproduction was based on fish held in cages. Yet unencumbered wild fish did not, in fact, spawn in the regions of appropriate copper concentrations because they avoided such concentrations. The fish moved downstream to lower concentrations, until stopped by a barrier, where they could go no further, and carried out their spawning.

The Schayler Run experiment also supports a fifth conclusion, that more emphasis on field experiments is desirable, to verify laboratory predictions.

A final conclusion concerns residues of cumulative toxicants in tissues. A higher proportion of effort should be centered on whether or not residues have any biological effects, not merely on chemical analyses of levels present in the tissues.

In closing, I should say that there is a multitude of recent papers not included in the blue book. I apologize to the authors, some of whom are present at this conference, for not reviewing the significance of their findings. For example, there have been excellent recent studies on swimming performance, avoidance reactions, reproduction, and internal physiological parameters. Perhaps some of these investigators can in the near future assemble and evaluate the new information in their field of work. Meanwhile, the present analysis may at least stimulate reaction on how to generate soundly based numbers to be used for controlling water pollution.

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Fish Tumors and Sublethal Effects of Pollutants[1]

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STICH, H. F., A. B. ACTON, AND C. R. FORRESTER. 1976. Fish tumors and sublethal effects of pollutants. J. Fish. Res. Board Can. 33: 1993–2001.

The feasibility of using fish tumors as an early, economic, and sensitive warning system for carcinogens in marine environments was examined. Two different tumor-fish systems were chosen: 1) papillomas among bottom-dwelling flatfish (Pleuronectidae) and 2) bilateral parabranchial tumors of the free-swimming Pacific cod (*Gadus macrocephalus*). Tumor prevalence can reach 58% among young English sole (*Parophrys vetulus*) and up to 100% in young cod populations. Tumor prevalence varies greatly (0.1–100%) in fish populations in various geographic locations. The possibility of involvement of virus and chemical carcinogens and the ease of screening large numbers seem to make fish tumors an ideal model of a situation that could easily develop in human populations within the foreseeable future.

STICH, H. F., A. B. ACTON, AND C. R. FORRESTER. 1976. Fish tumors and sublethal effects of pollutants. J. Fish. Res. Board Can. 33: 1993–2001.

Les auteurs étudient la possibilité d'utiliser les tumeurs de poisson comme système de pré-alerte avancé, économique et sensible de substances cancérigènes dans l'environnement marin. Ils ont choisi deux systèmes tumeur-poisson différents : 1) papillomes chez des poissons plats démersaux (Pleuronectidae) et 2) tumeurs parabranchiales bilatérales de la morue du Pacifique (*Gadus macrocephalus*) pélagique. L'incidence de tumeurs peut atteindre 58% chez les jeunes soles de Californie (*Parophrys vetulus*) et jusqu'à 100% dans les populations de jeunes morues. La prédominance de tumeurs varie grandement (de 0.1 à 100%) dans les populations de poissons de diverses régions. La possibilité que des virus ou des substances chimiques cancérigènes soient impliqués, ainsi que la facilité avec laquelle on peut examiner un grand nombre de poissons semblent faire des tumeurs de poisson un modèle idéal d'une situation qui pourrait facilement se présenter dans les populations humaines dans un avenir prévisible.

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USUALLY one associates cancer with man, affecting mainly persons during childhood and advanced age. Thus, it may come as a surprise to learn that cancer is a widespread disease among lower vertebrates or even invertebrates. Numerous cases of carcinomas and sarcomas of lower vertebrates, including fish, have been reported and are now being compiled by the Registry of Tumors in Lower Animals at the Smithsonian Institution (Harshbarger 1965–1975; 1972). In spite of these laudable efforts, our knowledge about the etiology of fish tumors and a possible relationship between tumor frequencies and man-made or naturally occurring contamination by carcinogens is meagre. This situation is partly due to the lack of attention given to cancer of nonhuman species and partly due to the difficulty of finding research personnel able to master pathology, cancer research, and fish biology. Nevertheless, studies of fish tumors may have great practical implications and are also of considerable theoretical interest. For example, cancer of commercially valuable species can, through adverse public reaction, have a serious economic effect. Fish may also represent a highly sensitive and economic organism suitable for large-scale

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TABLE 1. Occurrences of skin papillomas among Pleuronectidae and Bothidae of the Pacific Ocean.

Coast of North America		Coast of Japan	
Platichythys stellatus Starry flounder	McArn et al. 1968	*Limanda schrenki*	Oishi et al. 1975
		L. herzensteini	Kimura et al. 1967
Parophrys vetulus English sole	Wellings et al. 1965	*Hippoglossoides dubiuns*	Kimura et al. 1967
Hippoglossoides elassodon Flathead sole	Wellings et al. 1965	*Platichthys stellatus*	Oishi et al. 1975
	Wellings and Chuinard 1964	*Verasper moseri*	Oishi et al. 1975
Psettichthys melanostictus Sand sole	Nigrelli et al. 1965		
Microstomus pacificus Dover sole	Mearns and Sherwood 1974		
Lepidopsetta bilineata Rock sole	Own observations		
Glyptocephalus zachirus Rex sole	Wellings et al. 1965		
Isopsetta isolepis Butter sole	McArn et al. 1968		
Citharichthys stigmaeus Speckled sanddab	Own observations		

screening of chemical carcinogens or carcinogenic metabolites, following their passage through man (Campbell et al. 1974).

In this short review we would like to restrict the discussion to two tumor–fish systems: skin papillomas among flatfish species (Stich and Acton 1975) and parabranchial-gland tumors in the Pacific cod (*Gadus macrocephalus*) (Forrester 1969). An understanding of the biology of these two different tumors and fish populations may make it possible for us to decide whether fish tumors can be used as an early-warning system for the appearance and accumulation of carcinogenic agents, either in estuaries that are invaluable resources for aquaculture, or elsewhere. An in-depth analysis of the epidemiological results and their statistical evaluation will be published in more technically oriented papers.

Flatfish Species as Indicator Organisms

A suitable indicator organism must meet several prerequisites, including wide geographic distribution, abundance, absence of extensive migratory patterns, easy availability, uptake of carcinogens, and survival in polluted waters. Due to their particular habitat and behavior, flatfish species appeared to be worth careful consideration. Thus, we initiated a systematic study concerned with the feasibility of using flatfish as naturally occurring indicator organisms. Our first question dealt with the occurrence of skin papillomas among different flatfish species. This issue is of crucial importance because several species must be used to cover a wide spectrum of biotopes: deep vs. shallow areas, salt vs. brackish waters, various latitudes, mudflats, lagoons, etc. Obviously the Pleuronectidae would be useless as indicators if tumors were restricted to only one or a few species. A rapid perusal of the scientific literature, screening of museum specimens, and analysis of trawl collections revealed the occurrence of skin papillomas among several pleuronectids and bothids common in the inshore waters of the North Pacific (Table 1).

The second question concerned the geographic distribution of tumor-bearing flatfish species. A restriction of diseased fish to only one locality or habitat would seriously hamper the usefulness of these species for a possible global monitoring program. In spite of many "case reports" the precise distribution range of tumor-bearing flatfish is unknown. There seems to be little doubt that the occurrence of skin papillomas extends over wide regions of the North Pacific (Fig. 1), whereas their distribution among flatfish populations of the Atlantic Ocean is less well documented. Whether skin papillomas are restricted to the Pacific shorelines, whether the tumor incidence in Atlantic flatfish species is so low that only a large-scale sampling program could uncover them, or whether this difference in tumor incidence is only apparently caused by an accidental accumulation of fish-tumor experts in the Pacific Rim countries, are fundamental but at present unanswerable questions. Similar problems are also encountered by human epidemiologists who, in spite of the many imponderables, were finally able to reveal clustering of human leukemias, carcinomas, and sarcomas. By comparing sites with the highest tumor frequencies with regions having the lowest levels, it was possible

FIG. 1. Distribution of flatfish species with a high prevalence of skin papillomas; sand sole (*Psettichthys melanostictus*) data (Ketchen personal communication), starry flounders (*Platichthys stellatus*) (McArn and Wellings 1971), flathead sole (*Hippoglossoides elassodon*) Miller and Wellings 1971), and Dover sole (*Microstomus pacificus*) (Mearns and Sherwood 1974).

to suggest that environmental factors must be involved in more than 80% of human neoplasms (Oettlé 1964; Davies 1971). If we follow this line of thought, then we should also be able to uncover large differences in tumor incidences among fish populations when external factors are involved in their etiology.

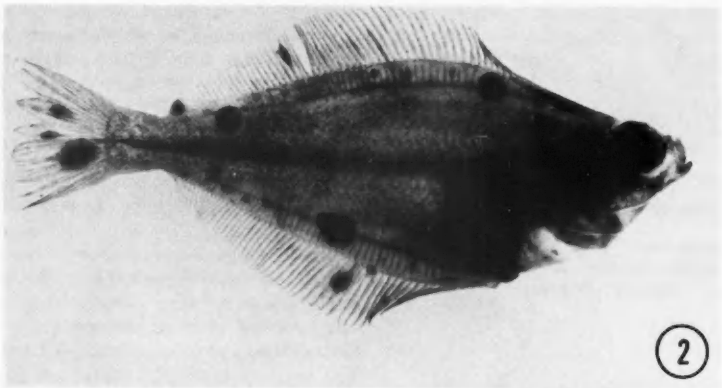
Use of Skin Papillomas as an Endpoint

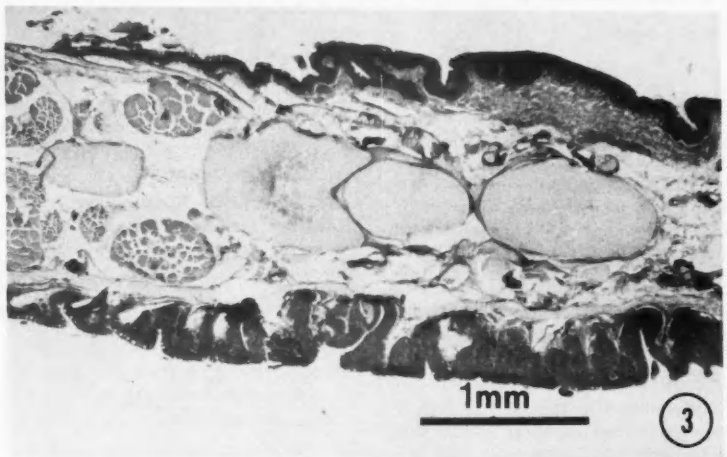
The selection of a simple endpoint which can be diagnosed without ambiguity, quantified and identified without the necessity of an autopsy is crucial to the successful application of a bioassay. After carefully weighing the pros and cons of internal tumors vs. external, we decided to concentrate on the well-known skin papillomas of flatfishes (Wellings 1969). This decision was mainly based on the following reasoning: 1) skin nodules and papillomas of flatfish can be counted on the entire fish, thus permitting a rapid screening of commercial catches; 2) the histology of these tumors revealed a clearly defined uniform pattern, thus making a cytopathological examination of each tumor superfluous; 3) a fair amount of background information was available, and 4) a large-scale epidemiological study can be pursued due to the cooperative effort of laboratories in Mexico, United States, Japan, and Canada. We would, however, be remiss if we did not mention the greatest drawback of employing skin papillomas as an endpoint, namely their unknown etiology.

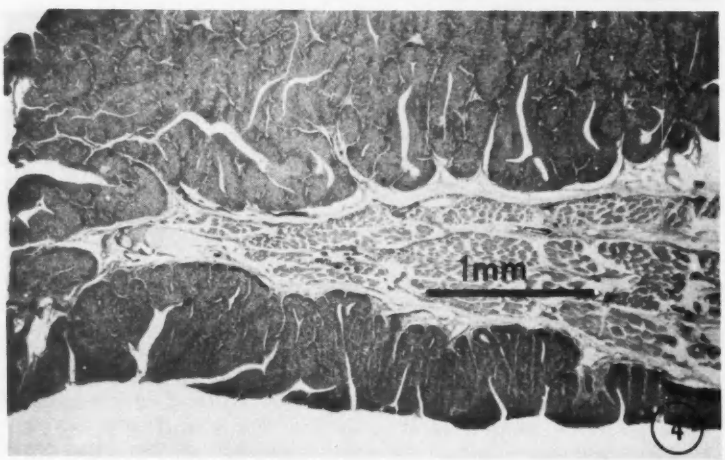
The histology of skin nodules and papillomas among various flatfish species closely resemble each other (Fig. 2). The nodules are small, smooth surfaced, vary from 1 to 5 mm across and may be white or red. They are composed of a multilayered hyperplastic epidermis which consists of typical epidermal cells above a relatively large accumulation of strongly vascularized connective tissue (Fig. 2, 3). The papilloma type of tumor is usually larger (10 mm and up) and has a raised surface (Fig. 3, 4). Some have diffuse and others clearly defined boundaries. The most characteristic feature of papillomas are giant cells with large nuclei and nucleoli (X-cells, Brooks et al. 1969) and so called "envelope cells" which seem to envelop the "giant" cells (Fig. 5, 6). There is also a third type of tumor which may be transitional between the first two. Virus-like particles (30 nm) identical in appearance to those reported by Pfizner and Schubert (1969) and Schubert (1969) in the European eel were found in some of the examined papillomas of English sole (*Parophrys vetulus*). Unfortunately, unless these particles appear in clumps, it is impossible to be sure of their existence since isolated particles are difficult to distinguish from other elements of the cytoplasm. We compared the macroscopic appearance with the microscopic histopathology on more than 210 tumors and feel confident that the classifying of these skin tumors by external appearance will lead to very little error in our survey.

Local Differences in Prevalence of Skin Papillomas Among Flatfish

Prior to discussing our epidemiological results we would like to mention a few possible sources of error. Since the skin papillomas of many flatfish species start to develop shortly after their metamorphosis, reach a peak usually within the 1st yr postmetamorphosis (there are species-specific variations), and decrease in frequency thereafter, all prevalence data must be age-adjusted. A good comparison could be achieved by using only the peak frequencies obtained at each sampling station. This procedure demands a precise knowledge of peak frequencies, which may vary according to geographic location and species. Thus, a single spot test can lead to gross underestimation of the actual tumor frequency when taken at a suboptimal time. Errors can easily arise, considering that the interval between low and high tumor prevalence can be less than

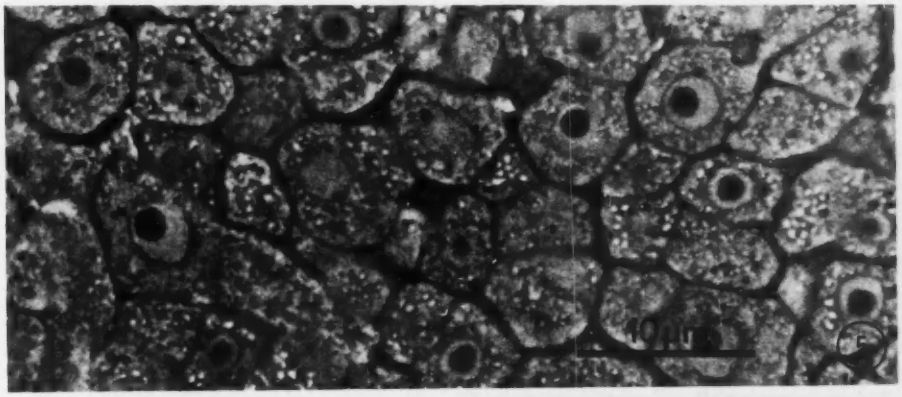


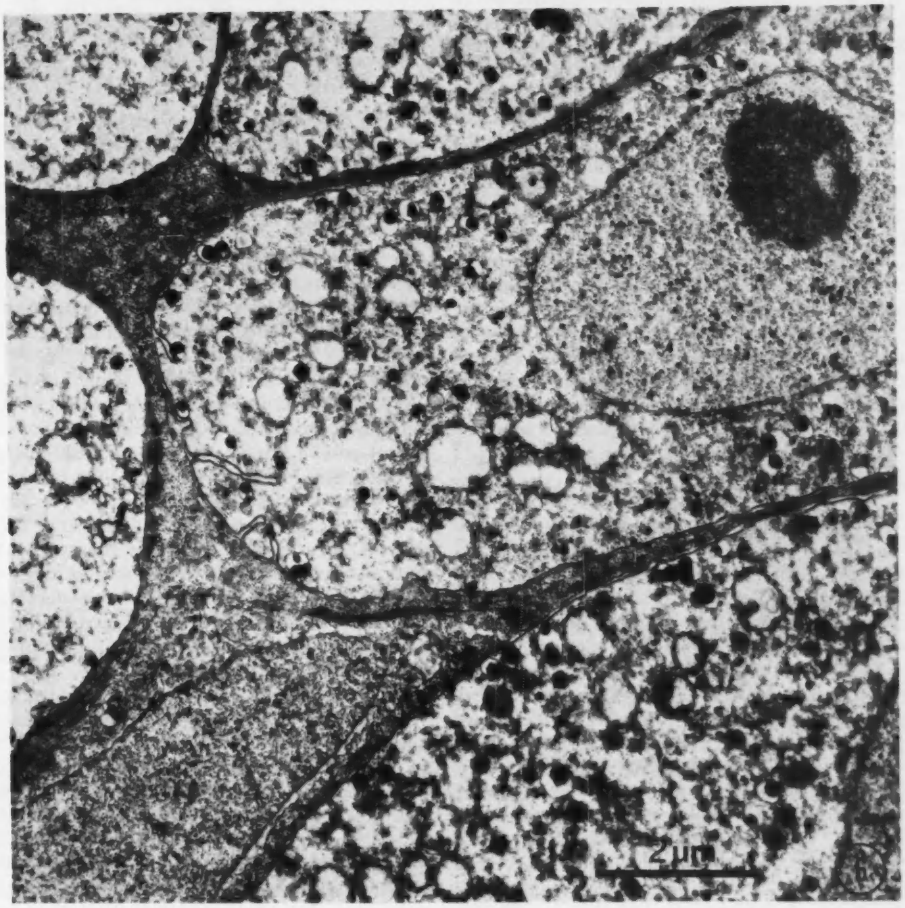




FIGURES 2–4

FIG. 2. Nine-centimeter English sole (*Parophrys vetulus*) with several skin tumors; FIG. 3. Section of a dorsal fin of English sole with skin tumors on both sides; FIG. 4. Section of papilloma of a 12-cm English sole.





FIGURES 5 AND 6

FIG. 5. Toluidine blue stained section of a papilloma which was embedded in epon. The "giant" cells with prominent nucleoli are surrounded by "envelope" cells. FIG. 6. Electron micrograph of several "pale" looking giant cells and dark envelope cells.

1 mo. To avoid a misleading interpretation we have taken monthly collections throughout the entire year when opening a sampling station. Only when the period of maximal tumor prevalence is known can the number of samples per year be drastically reduced. Another disturbing factor is a possible shift in the ratio between normal and tumor bearing fish due to a more rapid emigration of healthy specimens from nursery areas into deeper waters or to an excessive loss of the diseased fish to predators. Finally, there is always the question whether the examined group of fish is a proper representation of the fish population at large.

Tumor prevalence among English sole (*P. vetulus*) from different locations is shown in Fig. 7. There are two points of general interest: 1) The frequency of young fish with skin papillomas can be as high as 58%. This figure is extremely high as compared to the incidence of the most common human tumors which seldom exceeds 100 per 100,000 persons. 2) The differences between frequencies of skin papillomas are also much larger than one is used to seeing among human populations. They can vary between 0.1% (based on about 1,400 fish counted) and 58% (about 2,500 fish examined). 3) Tumor prevalence can differ considerably within relatively small distances (Fig. 8). 4) There seems to be a higher skin tumor frequency among English sole inhabiting areas of urban contamination (Vancouver) than among fish populations in regions remote from human activities (Qualicum Beach on Vancouver Island).

FIG. 7. Prevalence of skin papillomas among young postmetamorphosed English soles (*P. vetulus*) at different geographic locations. Data from San Francisco are from Cooper and Keller (1969), South California (A. J. Mearns and M. Sherwood personal communication), and Queen Charlotte Island (Ketchen personal communication; own observations).

Tumor Prevalence Among Different Flatfish Species

The great differences between tumor prevalences among various flatfish species is one of the unresolved issues. The extent of the variations observed at one location is shown in Table 2. The simplest interpretation would be to assume that the recorded differences in the prevalence of skin papillomas reflect different sensitivities among flatfish species. However, not all results support this notion. For example, 55% of starry flounders (*Platichthys stellatus*) collected in Bellingham Bay (McArn and Wellings 1971), which is only about 48 km from the sampling site mentioned in Table 2, show skin papillomas, compared with only 0.1% in the Vancouver area. Thus, starry flounders have a high capacity to develop skin papillomas and their virtual absence from specimens from the Vancouver region cannot be simply due to an inherent resistance. A similar argument can be applied to other species of flatfishes which show a low level of skin papillomas in the few samples taken. The immigration of older flatfish into a contaminated area could also easily lead to erroneous conclusions. As we have already previously discussed (Stich and Acton 1975), the sensitive period for papilloma induction may be restricted to the stage of metamorphosis, or earlier. Thus, older fish would not develop skin tumors even when they enter a contaminated area. If the assumption of a sensitive period during an early developmental stage is correct, then knowledge of the geographic distribution of flatfishes prior to and during metamorphosis becomes crucial. Of considerably less importance for tracing the etiology of skin papillomas is the location where the tumor bearing fish was actually caught.

Evidence points to a high sensitivity to developing skin papillomas among many, if not all, flatfish species and to environmental rather than to genetic factors for the observed differences in the tumor prevalences at different geographic locations. At present we know that the frequency of skin papillomas among young postmetamorphosed flatfish can reach the following levels: English sole (*Parophrys vetulus*) 58.6% (Stich and Acton 1975); starry flounders (*Platichthys stellatus*) 54% (McArn and Wellings 1971); a Japanese flounder, *Limanda schrenki*, 34% (Oishi et al. 1975); sand sole (*Psettichthys melanostic-*

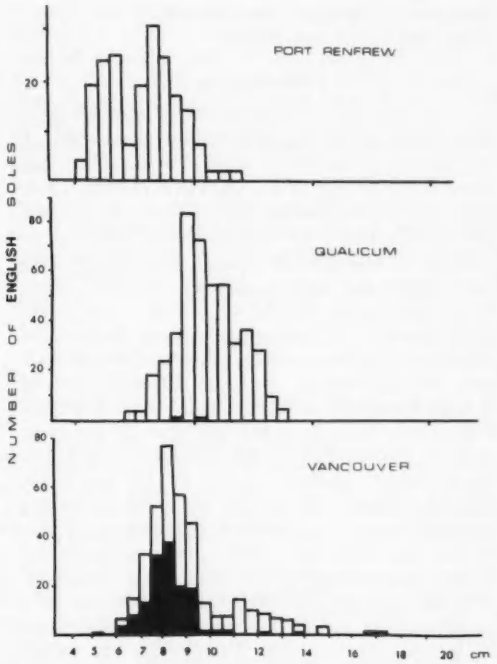


FIG. 8. Prevalence of skin papillomas among young English sole (*P. vetulus*) from relatively unpolluted areas (Port Renfrew, Qualicum Beach) and a contaminated region (Vancouver, North Arm Jetty). Solid black bars indicate number of tumor-bearing individuals.

TABLE 2. Prevalence of skin tumor among different Pleuronectidae and Bothidae species at one location (North Arm Jetty, Vancouver, B.C.) in 1974

	Max skin tumors among fish 1 yr post-metamorphosis	Avg no. tumors/fish
English sole	58.6%	6.8
Sand sole	22.5%	2.7
Dover sole	0.4%	1.0
Starry flounder	0.0%	—
Speckled sanddab	0.8%	1.0

tus) over 40% (Nigrelli et al. 1965); flathead sole (*Hippoglossoides elassodon*) 15% (Miller and Wellings 1971).

Tumor Prevalence in Pacific Cod from Coastal Waters of British Columbia

Tumors inside the gill covers were observed in Pacific cod (*G. macrocephalus*) from British Columbia trawl landings. These tumors, which resemble the type previously described by Wellings (1969) and Lange (1973), were always bilateral and so large on occasion that water flow through the gills must have been greatly reduced and size of food items swallowed limited.

A detailed study of the prevalence of this "carcinoid-like" (Lange 1973), or "parabranchial" (Wellings 1969) tumor in cod populations in various geographic areas was initiated. A total of 108,336 Pacific cod landed from various grounds were examined at ports of landing during 1968 to 1973. Variations in the mean tumor prevalences among cod populations are shown in Fig. 9. The figures presented express the tumor prevalence within the entire sample and therefore include fish of all age groups. No tumors were noted for 21,442 Pacific cod examined from the Strait of Georgia (region 4A in Fig. 9). For other areas off British Columbia, mean annual tumor prevalence increased northward from 4.5% off southwest Vancouver Island to a peak of 11.4% off Cape Scott. North of Cape Scott tumor prevalences were relatively low, varying from 2.4 to 3.0%. Examination of prevalence by month suggested that peaks in prevalence coincided with times of recruitment of new year-classes to the fishery.

In samples from all locations the tumor prevalence was highest in fish of small size and decreased with increasing length. In the area of highest overall prevalence off Cape Scott, tumor occurrence in samples ranged from 100% of small-sized fish to 0 at larger sizes. Mean tumor prevalence during 1968–73 averaged over 36%

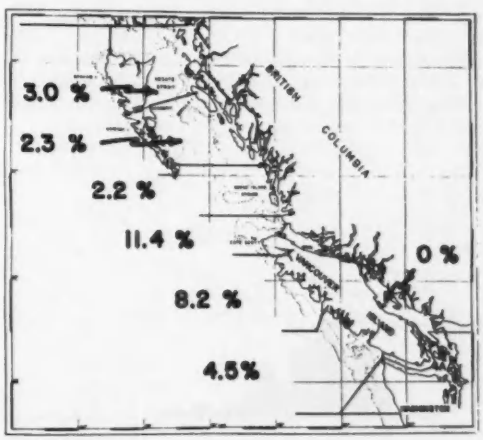


FIG. 9. Average tumor prevalence in Pacific cod (*Gadus macrocephalus*) populations from the coast of British Columbia.

in fish of 39–44-cm total length, dropped to less than 10% at sizes >66 cm and to 0 >76 cm.

In addition to sampling at ports of landing, sampling was also conducted aboard commercial vessels at sea off southwest Vancouver Island in March 1972 and March 1973. Tumor prevalence was 100% in fish of 29–34 cm, gradually dropped to a mean of about 25% at 45–52 cm and to 0 at sizes above 62 cm (Fig. 10).

Tumor presence may inhibit growth and maturation of the afflicted fish. Age determinations of two samples, taken in 1973 off Cape Scott, showed average length of tumor-bearing fish at each age to be slightly smaller than those without tumors. Also, modal sizes in tumor-bearing fish appeared to be lower than in those without tumors. In a sample of 407 fish from Hecate Strait, Levings (1968) found a significantly lower percentage of mature females >50 cm long and mature males of 50–65 cm long among the fish with tumors.

The sharp difference in prevalence of tumors between Pacific cod off Vancouver Island and those further north suggests the presence of separate stocks in these major regions and in the Strait of Georgia. This is supported by results of tagging studies which have shown virtually no interchange between fish in these regions. In Queen Charlotte Sound there are deep, almost transverse, gullies which probably restrict movement of the Pacific cod, known to be inhabitants of shallow and moderate depths (Smith and Forrester 1973).

The bilateral nature of the gill-cover tumors in Pacific cod, their growth to large size, the high prevalence observed in small fish, and the declining prevalence with fish size suggest that effects of the tumor may be an important component of natural mortality in juvenile fish (50% of Pacific cod males and 75–85% of females are immature at lengths <49 cm (Forrester 1969).

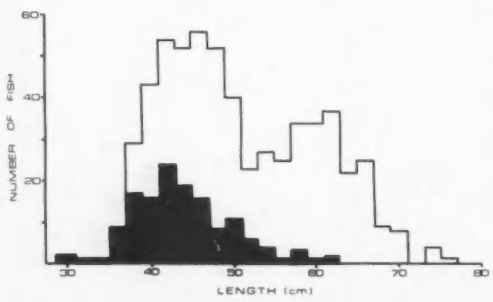


FIG. 10. Prevalence of parabranchial tumors in Pacific cod of various lengths.

However, this conclusion would be invalid if there was tumor regression.

Discussion

It has been repeatedly suggested that 80–85% of human carcinomas should be preventable if the carcinogenic agent could be identified and removed from man's environment (Oettlé 1964; Higginson 1969; Davies 1971). These conclusions are mainly based on epidemiological studies involving comparisons of human populations with the lowest and highest cancer incidence rates. Furthermore the tracing of tumor clusters and the diagnosis of "rare types" of neoplasm have recently uncovered several chemical compounds that induce cancer in man. Identification of β-naphthylamine affecting aniline dye workers (Hueber 1962), mustard gas among Japanese workers (Wada et al. 1968), inhalation of asbestos by textile workers (IARC 1973), and exposure of vinylchloride (IARC 1974–5) exemplify the usefulness of an epidemiologic approach. Unfortunately, little attention has been given so far to the epizootiology of cancer among nonhuman organisms. Even the presented results on skin papillomas among flatfish species and the parabranchial tumors of the Pacific cod are rather preliminary in nature. By choosing these particular tumor systems we attempted to illustrate two different patterns. Flatfish represent bottom dwellers with a restricted territory as compared to the free-swimming cod. Furthermore, there seems to be a link between prevalence of flatfish papillomas and discharges from human activity, whereas no such correlation can be observed with the cod tumors, which show the highest prevalence in fish populations inhabiting areas close to major sea-lion colonies. High prevalence of skin papillomas (up to 58% among young English sole) and parabranchial gland tumors (over 50% among 40-cm and shorter cod), the large differences in prevalence rates among populations from various geographic locations (from 0 to 58%), the bilateral occurrence of the parabranchial tumors of cod, the relatively large number of skin papillomas per flatfish, the strict age dependency of the two studied tumors, the possible involvement of viruses and chemical contaminants, and the ease of screening large numbers seem to make fish tumors ideal models of situations that could easily develop in human population within the foreseeable future.

Acknowledgments

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Reentry of 5-Year-Old Stranded Bunker C Fuel Oil from a Low-Energy Beach into the Water, Sediments, and Biota of Chedabucto Bay, Nova Scotia[1,2]

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VANDERMEULEN, J. H., AND D. C. GORDON JR. 1976. Reentry of 5-year-old stranded Bunker C fuel oil from a low-energy beach into the water, sediments, and biota of Chedabucto Bay, Nova Scotia. J. Fish. Res. Board Can. 33: 2002–2010.

Large amounts of Bunker C fuel oil remain stranded along the shoreline of Chedabucto Bay, Nova Scotia, 5 yr after the grounding of the Liberian tanker *Arrow*. This stranded oil is not static, but is slowly being released to the littoral and sublittoral environments. However, only trace amounts enter the tidal water column directly. The main route of reentry appears to be via the sediments and the interstitial water.

A parallel distribution to the low tidal–high interstitial oil distribution is found in tissue-bound oil in beach biota. High levels of Bunker C equivalents were found in the burrowing clam *Mya arenaria* and the rooted eelgrass *Zostera* sp. Such epibenthic organisms as the macroalga *Fucus* sp. contained no evidence of oil contamination. Very low levels were indicated in the mussel *Mytilus edulis*.

Beach sediments appear to act as a natural sink, sequestering interstitial oil (up to 10 mg oil/g sediment). Sediment-bound oil has a long residence time, and flow experiments indicate that stranded oil will remain in excess of 150 yr.

VANDERMEULEN, J. H., AND D. C. GORDON JR. 1976. Reentry of 5-year-old stranded Bunker C fuel oil from a low-energy beach into the water, sediments, and biota of Chedabucto Bay, Nova Scotia. J. Fish. Res. Board Can. 33: 2002–2010.

Cinq ans après l'échouage du pétrolier libérien *Arrow*, il y a encore de grandes quantités de fuel-oil « Bunker C » le long de la ligne de rivage de la baie Chédabouctou, Nouvelle-Ecosse. Ce pétrole n'est pas statique, mais est lentement mis en liberté dans les milieux littoraux et sublittoraux. Cependant, seulement des quantités minimes pénètrent directement dans la colonne d'eau de marée. La voie principale de rentrée semble être les sédiments et l'eau interstitielle.

On trouve une distribution parallèle (faibles quantités dans la colonne d'eau de marée–fortes quantités dans l'eau interstitielle) du pétrole fixé dans les tissus dans chaque biocénose. On a trouvé des niveaux élevés équivalents de fuel-oil « Bunker C » dans la mye fouisseuse *Mya arenaria* et dans la zostère marine enracinée *Zostera* sp. Des organismes épibenthiques, tels que la macro-algue *Fucus* sp. ne présentent aucun signe de contamination par le pétrole. De très faibles niveaux se rencontrent dans la moule *Mytilus edulis*.

Les sédiments de plage semblent agir comme puits naturel, emprisonnant le pétrole interstitiel (jusqu'à 10 mg de pétrole par g de sédiment). Le pétrole lié au sédiment a une longue durée de résidence, et des expériences d'écoulement démontrent que le pétrole gisant sur la plage persistera durant plus de 150 a.

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DESPITE all the research effort in recent years devoted to studying the environmental impact of oil pollution, except for the work of Blumer et al. (1973), little is known of the long-term fate of spilled oil stranded on shorelines. In this paper we present observations on the presence of weathered Bunker C fuel oil, spilled 5 yr previously, along the shoreline of Chedabucto Bay and on its reentry into the littoral and sublittoral environment.

At the time of the spill, February 4, 1970, the tanker *Arrow* released approximately 100,000 barrels (over 1 million gal) of Bunker C fuel oil. Much of this oil was transported by the prevailing winds and currents into the lagoons and estuaries around Chedabucto Bay, where it stranded on beaches and shorelines. Of 375 statute mi of shoreline, 190 mi had been contaminated in varying degrees (Anon. 1970). Despite a massive clean-up effort, a considerable amount of stranded oil was left to weather nat-

[1]Presented at the 13th Pacific Science Congress, Aquatic Resources Session, held at Vancouver, British Columbia, Canada, August 26, 1975.

[2]Bedford Institute of Oceanography Contribution.

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urally, much of which still remains (Thomas 1973).

We have examined the presence and the mobility of this stranded Bunker C fuel oil on a low-energy beach 5 yr after the *Arrow* spill. We discuss our findings in terms of the potential for reentry of stranded oil into the water column, and its long-term effects on the inshore environment.

Materials and Methods

Study Site

The beach study area was chosen because a) it formed part of a protected lagoon system flushed regularly by tidal action and supported a varied assemblage of both burrowing and epibenthic fauna and flora, and b) it was heavily contaminated by *Arrow* Bunker C fuel oil in 1970. The site lies on the south shore of Moussiliers Passage, a narrow channel connecting Haddock Harbor with Le Blanc Harbor (Fig. 1), part of the Janvrin lagoon system. The study site itself is a gently sloping beach, gravelled near the high tide line, and consisting of sand, mud, and gravel near the low tide region. The beach supports soft-shell clams, *Mya arenaria*, and mussels, the spermatophyte *Zostera* sp. and the macroalga *Fucus* sp., as well as a varied and plentiful assortment of smaller invertebrates, particularly *Polinices* sp., in the lower intertidal zone. Local inhabitants have continued to dig clams in this area for their own consumption up to the present day.

The study site consisted of a grid approximately 12 m² which extended from the high tide line down to the subtidal region at low tide (Fig. 2). Along the high tide line was a visible layer of tar 1–3 cm thick and 20–100 cm wide. During the first part of this study (October and November 1974) this entire tar zone was exposed and could be measured and sampled. During the latter part of the study (April and May 1975) the tar zone was covered by a layer of gravel, and could be located only by showelling aside the overlying gravel cover.

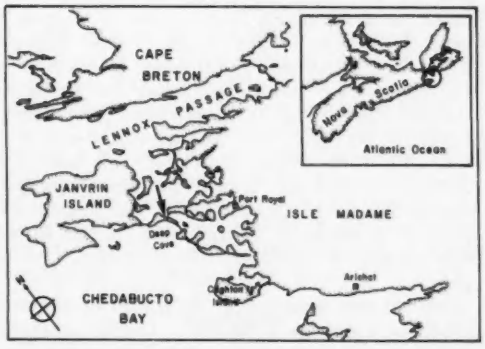

FIG. 1. Isle Madame–Janvrin Island area of Chedabucto Bay, showing lagoon system. Arrow indicates location of protected study site on Moussiliers Passage. Inset shows location of Chedabucto Bay, Nova Scotia.

Sampling and Oil Determinations

Water samples were taken along a transect at right angles to the shoreline. Water-column samples (2 liters) were collected, both at rising and falling tide, as near the water's edge as possible so as to contain oil "slicking off" the beach surface. Water-column samples were also taken several meters distant from the water's edge 15–20 m offshore. Water-column samples were collected by submersing solvent-rinsed glass bottles. All samples were collected in duplicate. Interstitial water samples (500 ml) were collected by scooping out water welling up in shallow pits dug just ahead of the advancing tide. Water samples were not filtered. Care was taken to avoid collecting particulate matter where possible.

Sediment samples (top 5 cm) were taken at five locations along the beach transect, approximately 2 m apart. These were immediately frozen in solvent-rinsed glass containers under dry ice. All samples were collected in duplicate.

Specimens of *Mya arenaria*, *Mytilus edulis*, *Zostera* sp., and *Fucus* sp. were obtained and maintained in insulated containers until analysis.

All samples were brought back to the laboratory for extraction and analysis within 48 h.

Two beaches near Dartmouth, Nova Scotia (Lawrencetown Beach/Porter's Lake inlet and Causeway Road beach) served as sources of uncontaminated water, sediment, and biota for control purposes.

All glassware and utensils were rinsed with distilled water, acetone, and either redistilled methylene chloride or redistilled hexane before use. Solvents were routinely checked for purity by fluorescence. In the field, all sampling apparatus was rinsed with redistilled solvent just before use. Great care was taken throughout field sampling to avoid contamination of samples.

Water samples were extracted by the method of Gordon and Keizer (1974). Sediment samples were

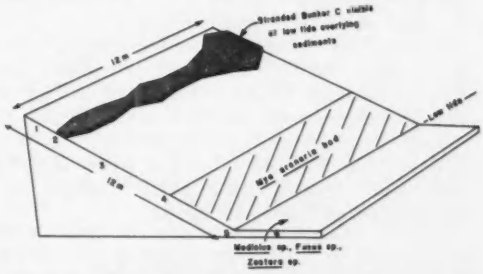

FIG. 2. Schematic of beach study site, showing tar zone along the upper high tide line and clam bed *Mya arenaria* on the lower beach slope. Slope of the beach is approximately 5°. Numbers along beach margin indicate sampling stations.

extracted directly into hexane on a wrist-action shaker (Hargrave and Phillips 1975). Clams and mussels, entire and dissected, were homogenized in redistilled hexane in a glass Duall tissue grinder. Algae were homogenized in an ultrasonic homogenizer (Polytron) and extracted with hexane. Hydrocarbon concentrations were determined in hexane in a Perkin-Elmer MPF-2A fluorescence spectrophotometer (Gordon and Keizer 1974). Results were exressed as Bunker C equivalents. Three-dimensional fluorescence spectra were prepared by the method of Hargrave and Phillips (1975).

Flow Study

Six glass trays (21 × 34 × 4 cm) containing oil-contaminated sediment from Station 4 (Fig. 2) were set up under constantly flowing sea water in the laboratory. The trays were positioned at a slight angle (10°), and water leaving the trays was collected at frequent intervals and analyzed for hydrocarbon content. Different flow rates, ranging from 3–40 liters/h, were used.

Results

Beach Survey

A preliminary inspection of 12 sites along the southern coastline of Isle Madame and Janvrin Island revealed visual evidence of oil in 11 out of the 12 beaches. Degree of contamination ranged from the appearance of an iridescent oil sheen on water filling shallow diggings (e.g. at Arichat Harbour and Babin's Cove) to tar deposits (2–3 cm thick) covering both rocky high-energy beaches (Crichton Island) and sheltered low-energy beaches (Moussiliers Passage). Tar deposits were found generally at the upper high tidemark. On rocky, exposed high-energy beaches the tar was found under boulders, and in the lee of rocky outcroppings in the upper spray zone. On more gently sloping, low-energy beaches the tar layer contained sediment and stranded kelp. In some places this layer formed a thick pavement 2–3 cm thick, with the consistency of a firm asphalt. Whereas the upper or exposed surface of stranded tar was covered by a rind of dull gray appearance, the tar in the underside or protected surface retained the glossy, sticky texture of freshly spilled oil. Tidal water washing over such deposits showed the brilliant iridescence of oil filming its surface.

Quantification of Oil at Study Site

The tar zone at the upper high tidemark comprised about 8.5 m^2, was approximately 2 cm thick, and covered approximately 85% of the beach surface. During the first part of the study when the tar layer was exposed, an oily slick spread downward from the tar zone over another 5% of the beach area. Stranded Bunker C oil comprised 11.6 ± 8% of this tar layer, the remainder (88.4 ± 8.1%, $N = 5$) being sand, fine gravel, and beach detritus. The three-dimensional fluorescence contour plot of a hexane extract of the stranded tar closely resembles that of the original Bunker C fuel oil carried by the *Arrow* (collected at the time of the spill and kept in cold storage at our laboratory) (Fig. 3). The fluorescence pattern shows the highly regular pattern of equal-intensity contours, with the single dominant peak at approximately 320–370 nm (excitation vs. emission).

Concentrations of oil detected in water and sediment are shown in Table 1. Concentrations in the water column, nearshore and offshore, are consistently in the μg/liter (ppb) range. Oil concentrations in the water column after the winter gravelling of the beach were considerably lower than in 1974 when the tar zone was exposed. Oil concentrations in interstitial water were higher than in the water column by three orders of magnitude, reaching maximum values in the samples taken from underneath the tar layer. In fact, interstitial oil content was at times so high that concentrations were obtained gravimetrically in tared round bottom flasks after evaporation of the organic solvent. Concentrations of oil in sediment again show considerable variation between samples, but all are in the milligrams per gram (parts per thousand) range. Highest concentrations were found directly under the tar layer and immediately down the beach slope from it. Concentrations in the sediments of the clam bed ranged between 0.7 and 1.5 mg/g.

Hydrocarbon concentrations in the tissues of bivalves and algae are shown in Table 2. High levels were found in the burrowing soft-shell clam *Mya arenaria* and in the rooted eelgrass *Zostera* sp. Specimens of *M. arenaria* taken from the upper clam bed area nearest the tar zone showed slightly higher values than those taken from further down the beach, nearer the low tidemark. Comparison of fluorescence contours of contaminated and noncontaminated *Mya* and *Zostera* (Fig. 4) clearly shows the single-peak pattern of Bunker C fuel oil masking the native fluorescence contours of noncontaminated samples.

No oil was detected in the tissues of *Mytilus edulis* or *Fucus* sp. (Table 2). The fluorescence contours of *Fucus* support this finding, the pattern of Moussiliers Passage specimens not differing significantly from that of control specimens. However, although initial quantitative analysis showed no fluorescence above background levels in *M. edulis*, the fluorescence contours contain

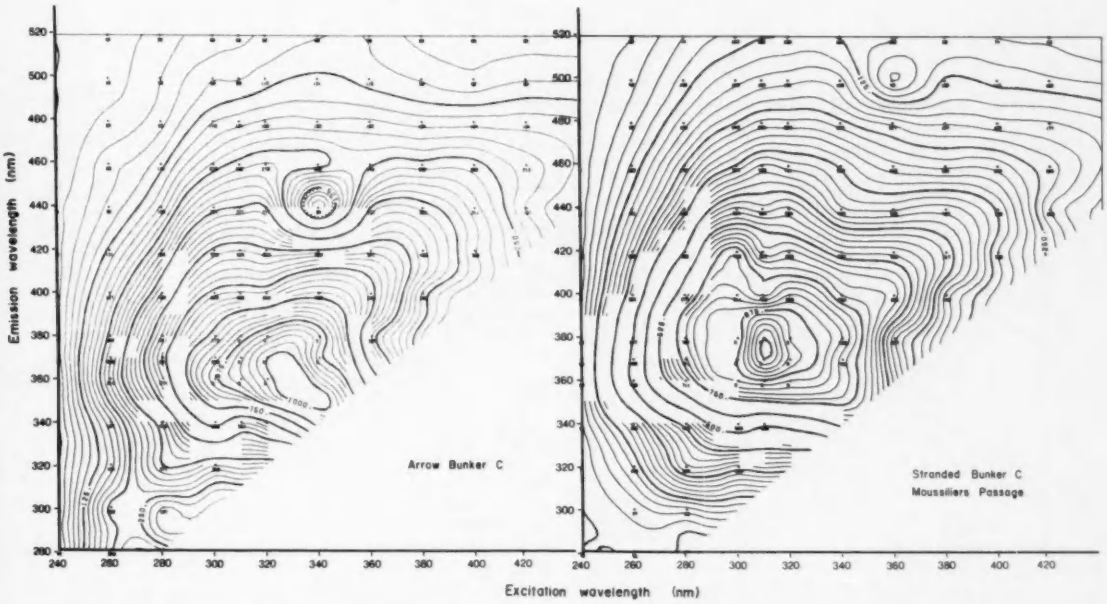

FIG. 3. Three-dimensional fluorescence intensity contour plots of *Arrow* Bunker C and of stranded tar taken from Moussiliers Passage, Chedabucto Bay, N.S. Note similarity in the regular pattern of equal intensity contours, and the single dominant fluorescence peak at ca. 320–360 nm.

the regularity of pattern found in Bunker C, unlike the irregular fluorescence pattern of native mussels, *M. edulis*.

Various physical data and estimates of total beach tar content are summarized in Table 3.

Flow Experiments

Results of the flow experiments are confounded by high variation of oil content between trays and between samples from one tray. However, concentrations of Bunker C released from the oiled beach sediments by flowing water are generally within the micrograms per liter (parts per billion) range (Table 4). This is similar to concentrations measured in the water column at the study site (Table 1). There appears to be little relationship between flow rate and oil release. A tenfold increase in flow rate did not significantly increase rate of release of oil from the sediment. Release averaged about 620 μg of oil/h.

Discussion

There is a considerable amount of weathered Bunker C fuel oil still remaining on Chedabucto Bay beaches 5 yr after the *Arrow* spill, and this stranded oil is not static, but is gradually reentering the littoral and sublittoral environments.

The tar layer stranded at the upper high tide mark, except for the weathered crust, is probably largely unaltered Bunker C fuel oil (Rashid 1974), although the minor differences in fluorescence contours between *Arrow* Bunker C and the stranded beach oil (Fig. 3) suggest some degree of weathering. However, the fluorescence technique is not conclusive, for it provides information about only one spectroscopic property of the oil (Gordon and Keizer 1974). The composition of the tar absorbed by the sediments is unknown. Preliminary examination of sediment-bound tar by GLC has shown marked differences in the n-alkane composition from that in *Arrow* Bunker C. Changes include disappearance of most of the n-alkanes below C_{28} and appearance of a number of unidentified hydrocarbons. Chromatograms were distinguished by a large envelope of unresolved peaks in the boiling range from C_{15} to C_{25}. These differences are suggestive of microbial activity and evaporation. Further, preliminary examination of synchronous excitation–emission spectra of sediment-bound tar has also shown differences from original Bunker C. The fate and transitional changes in composition of stranded Bunker C fuel oil are presently under investigation, and results will be reported at a later date. Nonetheless, whatever the precise nature of either

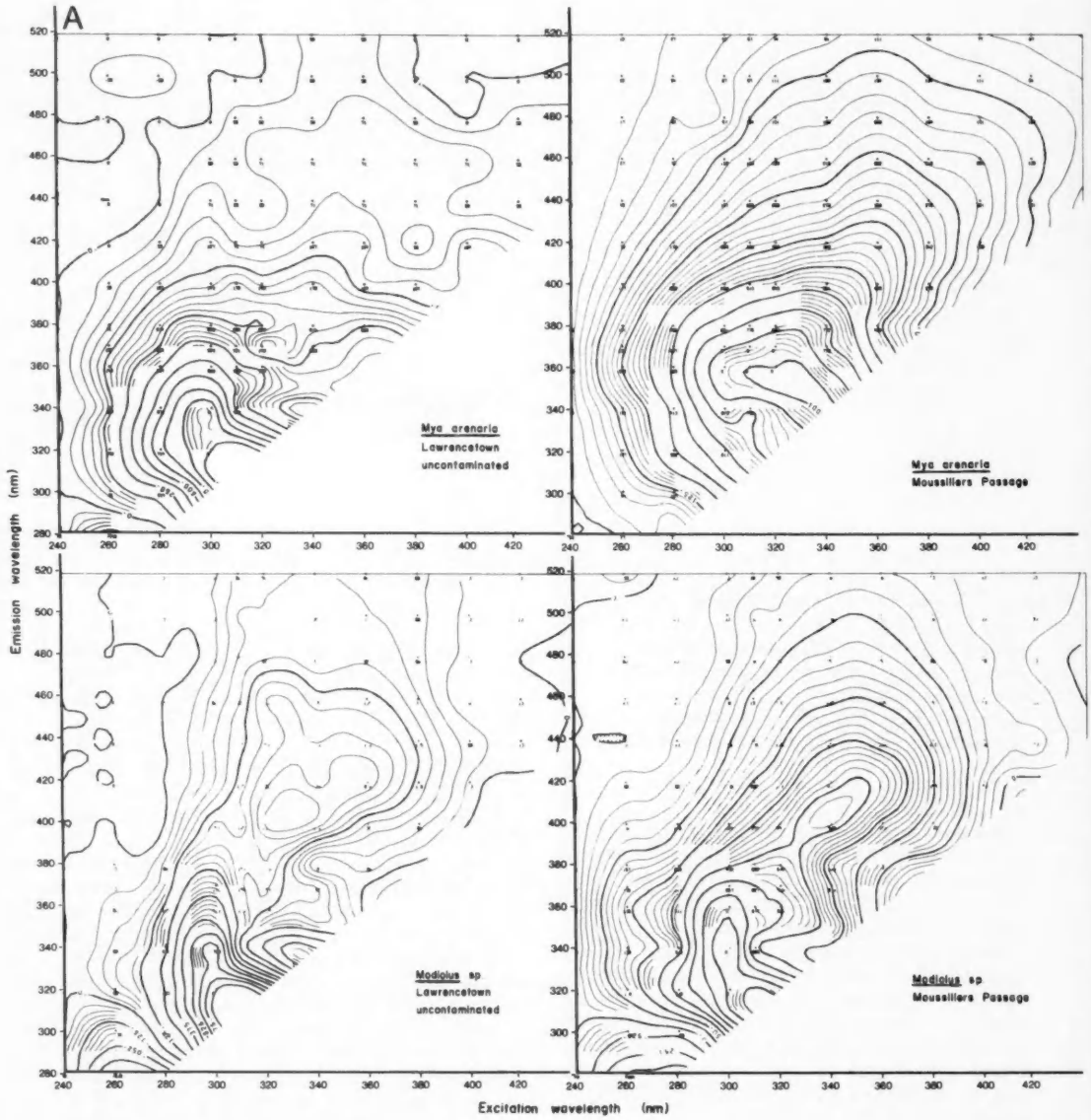

FIG. 4. Comparison of fluorescence intensity contour plots of bivalves and algae from an uncontaminated beach (Lawrencetown Beach/Porter's Lake inlet, N.S. — series at left) and from a Bunker C contaminated beach (Moussiliers Passage, Chedabucto Bay, N.S. — series on right). Note the masking of native fluorescence profiles by that due to Bunker C in (A) *M. arenaria, Mytilus* sp., and (B) *Zostera* sp., *Fucus* sp. does not show contamination. (Note: *Modiolus* sp. in the figure should read *Mytilus* sp.)

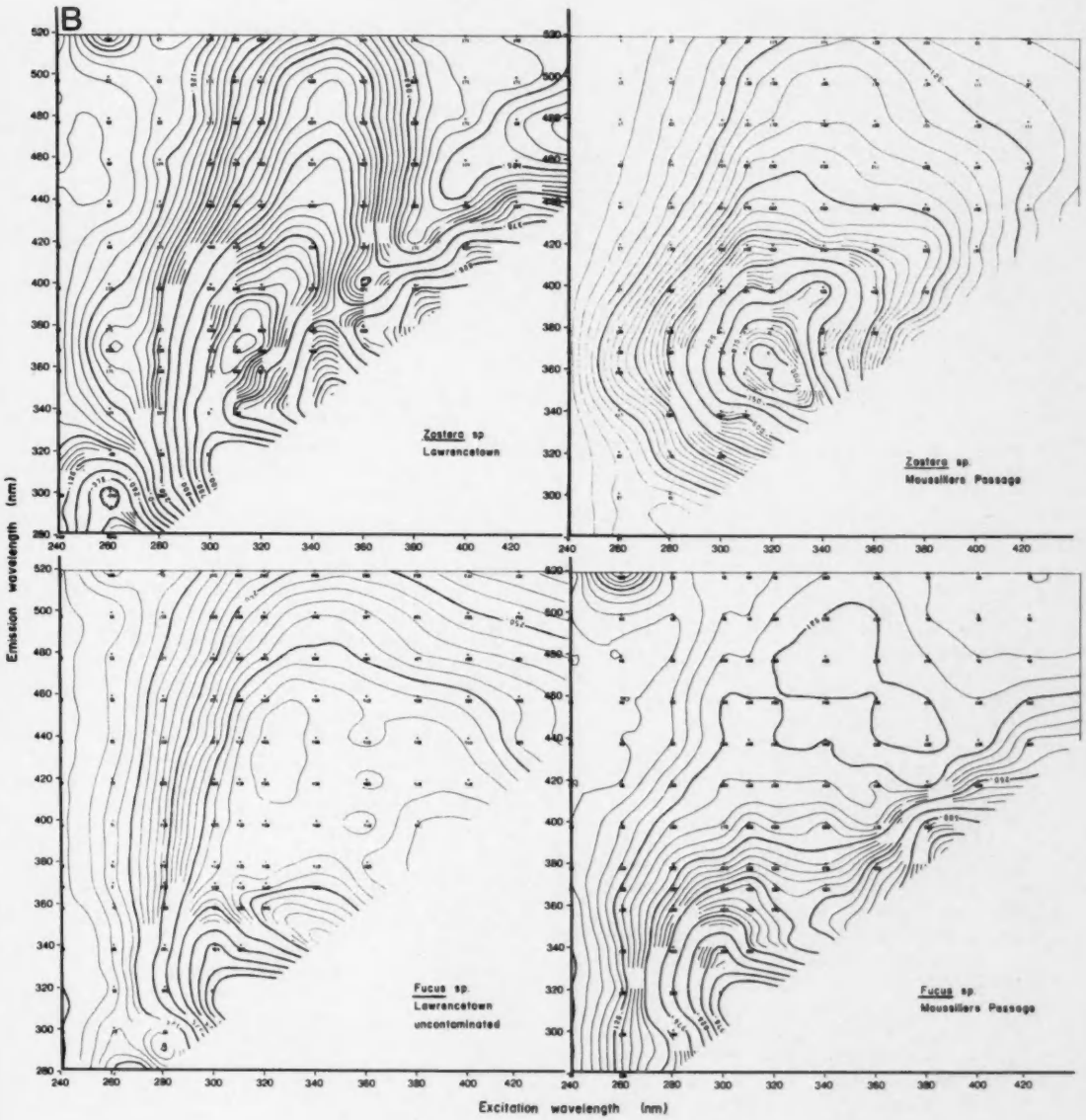
B
Zostera sp.
Lawrencetown
Zostera sp.
Mousaliers Passage
Fucus sp.
Lawrencetown
uncontaminated
Fucus sp.
Mousaliers Passage
Emission wavelength (nm)
Excitation wavelength (nm)

TABLE 1. Oil Concentrations (in Bunker C equivalents), detected using fluorescence spectroscopy, in water and sediments from Moussiliers Passage, Chedabucto Bay, Nova Scotia. See Fig. 2 for station locations. NA = data not available.

Station	Water column			
	Oct.–Nov. 1974[a] (*μg/liter*)	Apr.–May 1975[b] (*μg/liter*)	Interstitial water (*mg/liter*)	Sediment (*mg/mg*)
1	31	5–7	5–22	NA
2 (tar zone)	125	4–5	18–108	6.7–15.8
3	170	NA	NA	43.1–72.1
4 (upper *Mya* bed)	NA	5–6	95–269	0.7–1.5
5 (lower *Mya* bed)	28	1–2	11–91	0.04–0.11
6 (low tidemark)	3	1–2	NA	0.03–0.10
offshore — 1 m	1	1	NA	NA
offshore — 12 m	1	1	NA	NA

[a]Tar zone exposed.
[b]Tar zone covered.

TABLE 2. Bunker C fuel oil concentrations in bivalves' alga, and eelgrass from Moussiliers Passage, Chedabucto Bay, N.S.

	N	μg Bunker C/g wet wt.[a]
Mya arenaria		
upper beach	10	14.21±6.02
lower	10	12.40±4.03
Mytilus edulis	10	0
Fucus sp.	10	0
Zostera marina	10	17.13±8.18

[a]Bunker C concentrations determined by reading fluorescence intensities in hexane extracts (excitation 310 nm, emission 374 nm). Values were converted to Bunker C equivalents by comparison with a standard curve prepared from original *Arrow* Bunker C.

stranded tar in the tar zone or of sediment-bound tar, it is clear that a considerable amount of Bunker C type oil remains on the beaches. A similar persistence of a stranded light fuel oil and of two stranded paraffinic crude oils for at least several years has been reported by Blumer et al. (1973).

In view of this slow disappearance of stranded Bunker C, its fate with respect to the water column becomes important. Apparently, the main route of reentry is via the beach sediments and interstitial water, with minimal or even negligible amounts entering the water column directly. Also, subsequent release of hydrocarbon from the sediments into the water column appears to occur extremely slowly, judging by the results of our flow studies (Table 4). Even with large increases in flow rate, there is no significant parallel increase in hydrocarbon movement into the water stream. In fact, the sediments act as a large sink, imbibed oil having an extremely high residence time. This scheme is summarized in Fig. 5.

It is tempting to speculate on the time required for total removal of oil, that stranded at the high tidemark and that bound in the sediments, by tidal flushing. Information from the flow experiments suggests that at a flow rate of 40 liters/h, assuming linear loss, approximately 170 yr is required to completely flush out the tar contained in one of our experimental trays (ca. 900 g/tray) by water flow only. This is a very tenuous estimate and should be treated cautiously in attempts to extrapolate this figure to the problem of stranded tar in the field. Our experimental set-up differs from the real field situation in flow characteristics, in the absence of tidal erosion, in interstitial pumping due to tidal fluctuation, and other environmental parameters such as rainfall, wave action, etc. The situation is further compounded by the continued input of freshly leached oil from the tar zone at the high tide mark by daily tidal inflow. This large amount of stranded tar, acting as a slow-release source continuously replenishing sediment-bound tar will probably extend this time estimate considerably. However tenuous, the estimate does demonstrate that leaching of oil from sediments by water flow alone occurs very slowly, and emphasizes the extreme longevity of sediment-bound tar.

Biological Implications

Evidence to date indicates no discernible effects on marine phytoplankton by oil concentrations of 1 ppb as encountered offshore (Vandermeulen and Ahern 1975), or in the water column 1 m over the oiled beach. These concentrations are

TABLE 3. Summary of study site physical data and tar content calculations.

Physical data	
Dimensions (area)	12 × 12 m (144 m^2)
Tar zone area (vol)	8.46 m^2 (1.75 × 10^{-2} × 8.46 m^3)
Density of sediment	1.76 g/ml (1.6 × 10^3 kg/m^3)
Density of tar zone layer	1.17 g/ml (1.17 × 10^3 kg/m^3)
% tar in tar zone	11.6% (wt/wt)
Tar content	
Stranded tar zone	vol × wt × % tar = 20.36 kg
Sediment trapped	vol × sediment density × content
Station 1	0 kg
2	19.2
3	115.2
4	1.92
5	1.44
6	1.25
Total oil/study site	159.37 kg

TABLE 4. Release of sediment-trapped hydrocarbons to sea water flowing at different rates. Sediments contained 249.1±157.6 mg Bunker C equivalents/g sediment.

Flow rate (1/*h*)	Oil concn in water (μg/*liter*)	Bunker C eq released (μg/*h*)
3.5	22.69±32.40[a]	79.4
7.5	6.16±5.07	46.1
13.5	87.54±186.32	1181.3
23.0	2.42±2.04	55.7
26.2	0.33±0.47	8.6
37.9	31.23 (N = 1)	1174.9
42.2	56.98±95.03	2404.6
47.5	0.84±0.13	39.9
		$\bar{X}$ = 623.81 μg/h

[a] $N = 5$.

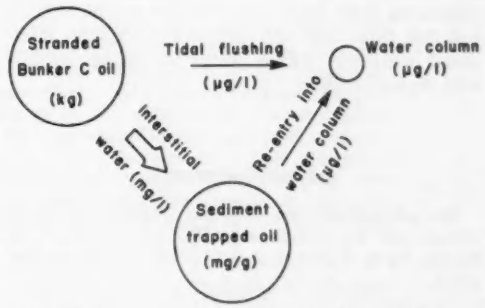

FIG. 5. Summary of stranded Bunker C fuel oil reentry pattern into marine environment. Concentrations given are range of magnitudes encountered in beach study site at Moussiliers Passage, Chedabucto Bay, N.S.

below those found inhibiting to photosynthesis in natural populations of phytoplankton (50 μg/liter, Gordon and Prouse 1973). These are also well below the levels found toxic or deleterious to larval stages of marine Crustacea (Boylan and Tripp 1971; Wells and Sprague 1976). Therefore planktonic components of the marine food chain probably experience little or no hydrocarbon insult directly. However, nothing is known of the potentially more devastating long-term effect of chronic exposure to low hydrocarbon concentrations. This question urgently needs study.

The situation is different for those organisms living at the sediment–water interface when concentrations of 200 μg/liter are encountered, or in the sediment, where interstitial concentrations are in the mg/liter range. Normal growth of newly hatched larvae of the lobster *Homarus americanus* released by the female is significantly depressed at concentrations of crude oil of 200 ppb (Wells and Sprague 1976). In our own laboratory we have monitored depression of respiration in the benthic crab *Callinectes* sp. at concentrations of 500 μg/liter Kuwait crude oil in sea water. Feeding behavior of *H. americanus* was found to be affected at concentrations of 10 ppm crude oil in sea water (Atema and Stein 1974). Although toxicity data on macroalgae due to oil is scarce, it is generally agreed that concentrations above 200–500 μg/liter are deleterious to plant growth (Vandermeulen and Ahern 1975). The problem of oil contamination of epibenthic and interstitial meiofauna is further magnified by their apparent inability to metabolize foreign molecules such as aromatic petroleum hydrocarbons. Unlike mammalian and teleost tissues (Stanton and Khan 1973; Orrenius and Ernster 1974; Payne and Penrose 1975), and possibly lobster (Elmamlouk et al. 1974; Gessner and Elmamlouk 1974),

which possess the enzyme system to metabolize various aromatic and polycyclic hydrocarbons, such mechanisms do not appear to exist nor are they inducible in such lower organisms as *Mya arenaria* or *Mytilus edulis* (J. H. Vandermeulen and W. R. Penrose unpublished data). Organisms at the sediment–water interface or existing within the contaminated sediment therefore accumulate a hydrocarbon load.

Finally, an aspect of oil pollution that has received little attention is the question of the effect of physical stabilization of a beach by oil on the overall productivity of an estuary or lagoon. Low-energy beaches, particularly in highly productive areas such as lagoons, support a rich and highly varied microfauna and microflora, subtly adapted to a dynamic, constantly shifting environment, the beach sediment. Reduced mobility of the beach substrate through permeation of the gravel–sand bed with tar will have concomitant effects on pore water oxygenation and interstitial nutrient flow, and will seriously affect the interstitial ecosystem. The problem becomes magnified with repeated spills.

Acknowledgments

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Epidermal Papillomas of Flatfish in the Coastal Waters of Hokkaido, Japan[1]

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OISHI, K., F. YAMAZAKI, AND T. HARADA. 1976. Epidermal papillomas of flatfish in the coastal waters of Hokkaido, Japan. J. Fish. Res. Board Can. 33: 2011–2017.

In the eastern parts of Hokkaido Island, Japan, epidermal lesions have been frequently found on flatfish. These were diagnosed as papillomas resulting from an abnormal proliferation of epidermal cells and were found on both the eyed and eyeless sides. Some of the cells were hypertrophied and irregularly shaped. Mucus secretion was decreased and there was only a weak reaction to periodic acid-Schiff (PAS) staining. A possible association between a blood-red parasite, probably *Philometra mariae*, and the development of the tumorous tissue was examined. The ratios of tumorous fish to total catch were 60:724 (8.29%) in inlets, and 43:12,600 (0.34%) in areas facing a strait. *Philometra* infection rates were 80:225 (35.6%) in the inlets, and 41:2,521 (1.63%) in the latter areas.

OISHI, K., F. YAMAZAKI, AND T. HARADA. 1976. Epidermal papillomas of flatfish in the coastal waters of Hokkaido, Japan. J. Fish. Res. Board Can. 33: 2011–2017.

Dans les parties orientales de l'île Hokkaidō, Japon, on trouve fréquemment des lésions épidermiques chez les poissons plats. Ces lésions ont été diagnostiquées comme étant des papillomes résultant d'une prolifération anormale de cellules épidermiques et se trouvant à la fois sur le flanc oculé et sur le flanc opposé. Quelques cellules sont hypertrophiées et de formes irrégulières. La sécrétion de mucus diminue et il n'y a qu'une faible réaction à la coloration à l'acide périodique Schiff (APS). Nous examinons la possibilité d'une association entre un parasite rouge sang, probablement *Philometra mariae*, et le développement de tissus affectés de tumeurs. Le rapport des poissons affectés de tumeurs à la prise totale est de 60:724 (8.29%) dans les petites baies et de 43:12000 (0.34%) dans les régions faisant face à un détroit. Les taux d'infection par *Philometra* sont de 80:225 (35.6%) dans les petites baies et de 41:2521 (1.63%) dans ces dernières régions.

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SKIN tumors of flatfish have been repeatedly analysed: Johnstone (1912) found skin tumors on the Atlantic halibut (*Hippoglossus hippoglossus*), Wellings et al. (1964) observed epidermal papillomas and angioepithelial nodules on flathead sole (*Hippoglossoides elassodon*) from San Juan Island, Washington, USA; Cooper and Keller (1969) examined papillomas on the English sole (*Parophrys vetulus*) of San Francisco Bay, California, USA; Mearns and Sherwood (1974) reported skin tumors and fin erosion of the Dover sole (*Microstomus pacificus*) from the coastal waters of Los Angeles, California; and Stich and Acton (1975) analysed nodules and papillomas of several flatfish species of British Columbia, Canada. In Japan, Kimura et al. (1967) investigated neoplasia of flatfish from Wakasa Bay, Honshu, and Awakura (1974) briefly described the histology of skin tumors of flatfish which were collected from the coastal waters of Hokkaido.

In this study, we report an epizootiological and histological analysis of skin tumors among several flatfish populations of coastal waters of Hokkaido Island, Japan. The main objectives of this study were to clarify what factors cause tumors in fish, how tumorous fish are distributed, and whether or not the skin tumor would be useful as a monitoring system for environmental pollution. Furthermore, we examined the possible relationship between skin tumors and a parasite (*Philometra mariae*), which mainly infects the fins of various flatfish species.

Materials and Methods

Fish samples were taken from the coastal waters of the eastern parts of Hokkaido, from the town of Chashikotsu to Furen Lake (Fig. 1). These districts are free of industrial contamination. They represent mainly agricultural and stock-farming areas. The drainage areas of the rivers flowing into the bays are

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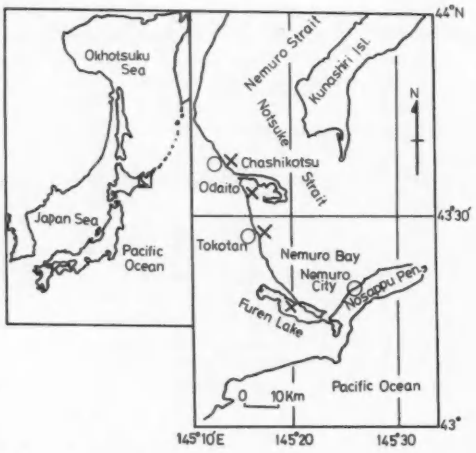


FIG. 1. Locations where flatfish, *Limanda schrenki* (includes *Liopsetta* sp.) were collected, are indicated by (x).

covered with peat moss. In this study, we divided the area into: 1) an inlet with stagnant water and 2) the strait with an active water circulation. The former is represented by the shallow Odaito Inlet, surrounded by Notsuke Peninsula, and the brackish Furen Lake. The strait areas are on the coast of Chashikotsu and Tokotan, facing Notsuke Strait between Hokkaido and Kunashiri Island. This strait, which is about 30 km wide, connects the Okhotsuku Sea with the Pacific Ocean.

Flatfish were collected by setting nets of 12–15-m length and 7-m width at 50–600 m offshore in 3–5 m of water. Fish collected in the net were flatfish, cod, *Sebastes*, salmon, stickleback, and others. Among these, tumors were most frequently found on the flatfish. Tumorous and nontumorous fish were separated, their numbers counted, and total length and body height measured. Small pieces of the skin tumors were removed and fixed with Bouin's solution for histological observation. Sections were made by the usual paraffin methods, cut in 10-μm sections, and stained with Delafield's hematoxylin and eosin. PAS staining was also used in some sections to detect the presence of polysaccharides.

Parasites in cysts were removed with forceps from the fish's surface. After measuring the dimensions of the cysts, we removed the parasites. Ovaries of parasites were observed by light microscope.

Results and Discussion

Two of the tumor-bearing flatfish (*Limanda schrenki*) are shown in Fig. 2 and 3. Neoplastic growth of the epidermis can be easily diagnosed in histological cross sections (Fig. 4). The melanocytes are arranged regularly along the connective tissue lining just below the epidermis. The total number of flatfish collected and the number of fish with skin tumors are given in Table 1. Skin tumors were virtually restricted to three species: *L. schrenki*, *Platichthys stellatus* and *Verasper moseri*. Fish specimens which we diagnosed as *L. schrenki* may also include *Liopsetta* sp. since the identification and separation of these two species is difficult according to the keys described by Matsubara (1955). Tumorous flatfish were found at a higher frequency in the inlet waters than in the strait: the ratio of tumorous flatfish to all flatfish caught was 60:724 (8.29%) in the inlet as compared to 43:12,600 (0.34%) in the strait.

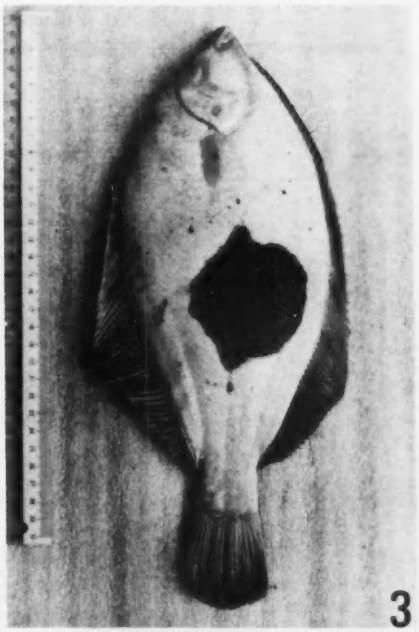
Blood-red nematodes of the family Philometridae were found in cysts which were located mainly on the fins of *Limanda schrenki* (Fig. 5). The parasites closely resemble *Philometra mariae*, described by Layman (1930) and Machida (1970). The size of the fixed adults was 22.6–29.0 mm long and 1.3–1.9 mm wide. They were encapsulated in oval cysts, 10–13 mm long and 3.5–4.0 mm wide. The parasite had a mouth with three labia but had no anus. All of the specimens in cysts longer than 5 mm were female and had a large ovary. The parasites in cysts of 3–4-mm length had neither eggs nor larvae. The ovary was filled with approximately a 100,000 eggs, embryos, and larvae. The eggs and embryos of the parasite were about 10 μm diam. The larvae were 350–400 μm in body length, 15 μm in width. A number of flatfish erythrocytes were observed in the intestines of parasites.

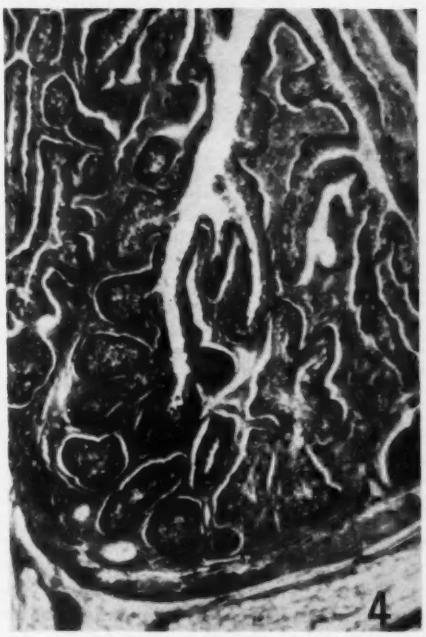
Size distribution of the skin papillomas is shown in Fig. 6, where size is represented by the longest diameter of the tumor. The left-hand ordinate of Fig. 6 indicates the number of tumors using a normal-distribution function. The linearity of these plots suggests that the size distribution of the tumors is Gaussian.

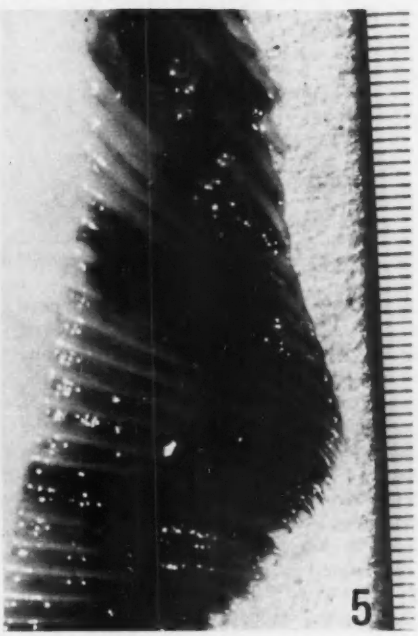
The length distribution of tumorous fish is shown in Fig. 7. Spin papillomas occur mainly on fish less than 18 cm long. The average area of the papillary lesions was 25 cm^2, ranging from 7 to 40 cm^2. They occupied about 12% (range 1–26%) of the total fish surface. No flatfish that had a tumor area greater than 30% of the body surface were collected. The fish would probably die before the tumor had covered more than 30% of the body surface.

The examined epidermal papillomas appear to be benign neoplasms. They do not form metastases and appear to proliferate slowly. The tissues of skin papillomas were easily torn and hemorrhaging lesions were frequently observed on tumorous parts of the fish.

The number of skin tumors per fish ranged







FIGURES 2–5

FIG. 2. *Limanda schrenki* with an epidermal papilloma at the head on the eyed side; Fig. 3. *Limanda schrenki* with an epidermal papilloma on the eyeless side; FIG. 4. Section of epidermal papilloma. Note the abnormal proliferation of the epidermis. ×50; FIG. 5. *Philometra mariae* in the cysts infecting the dorsal fin of the flatfish, *L. schrenki*.

TABLE 1. List of tumor-bearing fish collected.

Total no. in catch	No. of tumorous fish	Fish species	Collection date	Collection site
25	5	*Limanda schrenki*[a]	July 25, 1974	Furen L.
—	5	"	Oct. 6, 1974	"
—	1	*Platichythys stellatus*	Oct. –, 1974	Yoichi T.
—	2	*L. schrenki*[a]	Dec. 12, 1974	Odaito
—	1	"	Dec. 21, 1974	Tokotan
9	0	"	Dec. 19, 1974	Odaito
260	2	*P. stellatus*	Apr. 28, 1975	Akkeshi T.
—	1	*L.schrenki*[a]	"	Sanbongi
917	2	"	Apr. 29, 1975	Tokotan
1981	3	"	"	"
84	12	"	"	Odaito
7	0	"	Apr. 30, 1975	Tokotan
935	5	"	"	"
59	3	"	"	"
—	3	"	"	"
220	7	"	"	Odaito
17	1	"	"	"
1477	7	"	May 1, 1975	Tokotan
—	1	*Verasper moseri*	"	"
—	3	*L.schrenki*[a]	"	"
—	3	"	"	"
36	0	"	"	"
—	12	"	"	Betsukai T.
700	1	"	"	Tokotan
50	0	"	"	"
—	1	"	May 2, 1975	"
119	2	"	"	Chashikotsu
15	0	"	"	"
1265	2	"	"	"
116	18	"	"	Odaito
4900	13	"	"	Tokotan
139	5	"	"	"
253	17	"	May 3, 1975	Odaito

[a]*Limanda schrenki* includes *L. schrenki* and *Liopsetta* sp.

from 1 to 3, averaging 1.25. A total of 57 tumors occupied the eyeless side, 24 were on the eyed sides, and 68 spread to both sides. These results show that tumors occur more frequently on the eyeless than on the eyed side.

Histological studies revealed hyperplasia of the fibrous connective tissue in the lesions of the dermis and an increased number of epidermal cells that showed an irregular arrangement. Some of the hypertrophied cells varied greatly in shape. Secretion of mucous material by the secretory cells in the epidermis had deteriorated, and reacted only weakly with the PAS stain. The histological observations indicate that the papillomas resulted from an abnormal proliferation of epidermal cells.

The prevalence of flatfish infected with *P. mariae*, was 35.6% in the inlet and 1.63% in the strait. Parasites preferentially infected the eyeless side of the fish (Table 2); 47 fish had parasites on the eyeless side, 75 fish on both sides. There were no fish with parasites only on the eyed side. The number of the parasites found was 804 on the eyeless side, 223 on the other.

The number of parasites per fish which were collected at different places in eastern Hokkaido ranged from 1 to 42, with an average of 8.7 parasites per fish (Table 3). Fish of medium length (12–16 cm) were most frequently infected by parasites (Fig. 8). There seems to be a correlation between the occurrence of skin tumors and that of parasites. The prevalences obtained in different locations are shown in Table 4. The prevalence of tumors in fish populations of the inlet was 24 times, and that of parasites, 22 times, higher than those observed among fish from the strait.

Many tumors were observed at the base of the fins, indicating that they had developed from a point between the skin and body. Parasites also

TABLE 2. Distribution of the parasite *Philometra mariae* on various parts of the flatfish *Limanda schrenki*.

	No. of parasites					
	Odaito			Tokotan		
Body parts	Apr. 29	Apr. 30	May 2	Apr. 30	May 1	May 1
Eyeless side	183	35	341	239	3	3
Dorsal fin	99	20	198	130	1	1
Anal fin	73	15	117	94	2	2
Branchial membrane	9	0	21	12	0	0
Head	1	0	5	1	0	0
Caudal fin	1	0	0	2	0	0
Eyed side	41	13	108	55	3	3
Dorsal fin	29	6	58	34	3	0
Anal fin	12	7	35	17	0	0
Branchial membrane	0	0	15	4	0	3

TABLE 3. Parasite distribution per fish at various collection sites.

	No. of fish					
No. of parasites per fish	Odaito			Tokotan		
	Apr. 29	Apr. 30	May 2	Apr. 30	May 1	May 1
0	72	12	61	954	1477	49
1	2	1	3	6	0	0
2	3	0	7	4	0	0
3	7	0	0	1	0	1
4	5	1	1	5	0	
5	4	0	2	3	0	
6	1	0	3	1	1	
7	1	1	4	2		
8	2	0	0	3		
9	3	1	1	1		
10	1	0	1	3		
11	1	0	0	0		
12	3	0	1	3		
13	1	0	0	2		
14	0	0	3	2		
15	1	0	1	0		
16	0	0	1	0		
17	1	0	0	1		
19	0	0	1	0		
20	1	0	1	0		
21		0	2	0		
24		0	1	0		
25		0	2	0		
26		0	0	2		
29		1	0			
33			1			
36			1			
42			1			

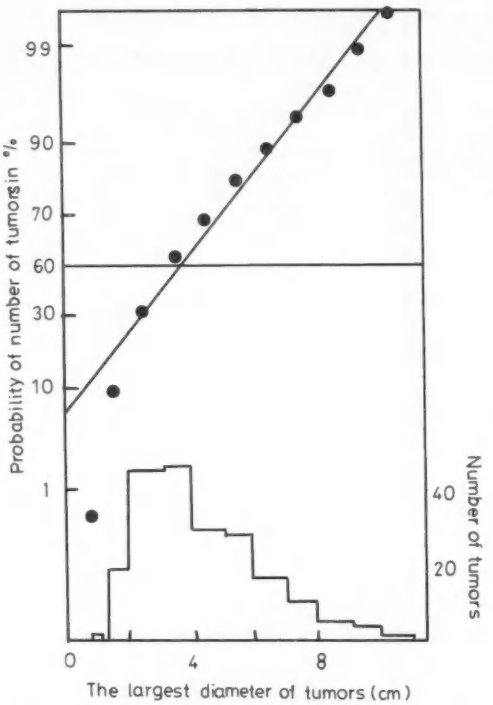


FIG. 6. Size distribution of skin tumors (*L. schrenki*).

TABLE 4. Comparison of the frequencies of flatfish (*L. schrenki*) bearing tumors or parasites in each locality.

	Locality	
	Inlet	Strait
Tumor-bearing	5:25 (20.0)[a]	2:917 (0.22)[a]
	0:9 (0.0)	3:1981 (0.15)
	12:84 (14.3)	0:7 (0.0)
	7:220 (3.2)	5:935 (0.53)
	1:17 (5.9)	3:59 (5.1)
	18:116 (15.5)	7:1477 (0.47)
	17:253 (6.72)	0:36 (0.0)
		1:700 (0.14)
		0:50 (0.0)
		2:119 (1.7)
		0:15 (0.0)
		2:1265 (0.16)
		13:4900 (0.27)
		5:139 (3.6)
	37:109 (33.9)	39:993 (3.92)
Parasite-infected	5:17 (29.4)	1:1478 (0.07)
	38:99 (38.4)	1:50 (2.00)

[a]Number of affected flatfish vs. total flatfish collected. The figures in parentheses are in percent.

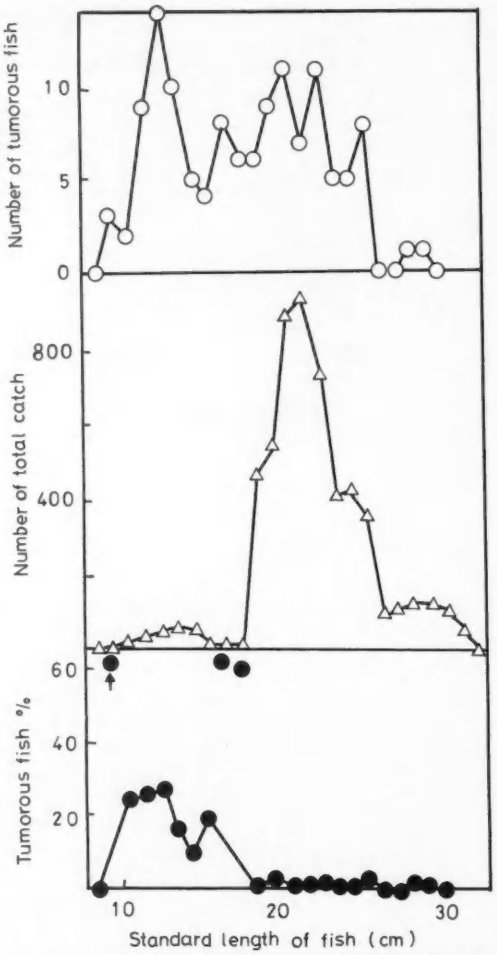


FIG. 7. Size distribution of tumorous fish (*L. schrenki*).

preferentially infected the fin. Tumors and parasites were found more on the eyeless side than on the other. This may be related to the behavior of flatfish, which come in contact with the bottom sediments with the eyeless side. There are, however, several differences between tumor development and parasite infection. Tumors were mainly observed in the smaller fish, whereas parasites occurred mainly in the medium-sized flatfish. Fish with tumors and parasites were only rarely observed. According to Nakajima et al. (1970), *Philometroides seriolae*, which infects the muscles of the yellowtail (*Seriola quinqueradiata*), produces larvae in the summer. Only if the life cycle of *Philometra mariae* becomes fully known will

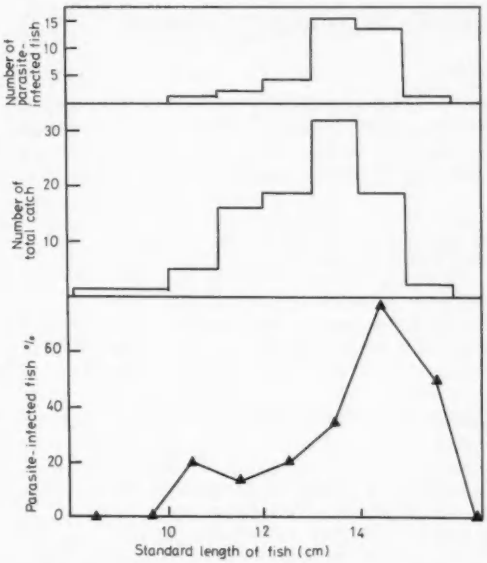


FIG. 8. Size distribution of the flatfish infected with *P. mariae*.

it be possible to analyse the relationship between parasite infection and tumor development.

Stich and Acton (1975) and Stich et al. (1976) have proposed to use the prevalence of skin tumors of flatfish species as a monitoring system for water contaminated by carcinogenic agents. The results obtained in this study show that at least three flatfish species which inhabit areas free of industrial and municipal discharges are afflicted by skin tumors. If the skin papillomas of flatfish are induced by environmental factors at all, then we must consider the involvement of naturally occurring contaminants as well as man-made pollutants in the etiology of these neoplasms. Whether the high prevalence of skin tumors and parasites in the flatfish of a particular region indicates a contamination that may be hazardous to man needs further study.

Acknowledgments

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Effects of Polluting Substances on Enzymes of Aquatic Organisms[1,2]

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BROWN, G. W. JR. 1976. Effects of polluting substances on enzymes of aquatic organisms. J. Fish. Res. Board Can. 33: 2018–2022.

The toxicity of heavy metal cations often considered as pollutants is discussed with respect to several enzymes of nitrogen metabolism in the trout *Salmo gairdneri* and the polychaete *Eudistylia vancouveri*. Data on trout liver ornithine aminotransferase (EC 2.6.1.13) activity under inhibition by mercuric ion yield a straight line when percent inhibition on a probability axis is plotted vs. logarithm of mercuric ion concentration. Allantoinase (EC 3.5.2.5) of *E. vancouveri* is inhibited by divalent cations of Cu, Hg, Zn, Pb, and Cd. At low concentrations ($\sim 10^{-8}$M) these ions lead to an enhancement of activity of allantoinase. A short review is provided on the adaptation of fish to environmental changes.

BROWN, G. W. JR. 1976. Effects of polluting substances on enzymes of aquatic organisms. J. Fish. Res. Board Can. 33: 2018–2022.

Nous analysons la toxicité des cations de métaux lourds souvent considérés comme polluants en rapport avec plusieurs enzymes du métabolisme de l'azote chez la truite *Salmo gairdneri*, et le polychète *Eudistylia vancouveri*. Les données sur l'activité de l'ornithine aminotransférase (EC 2.6.1.13) du foie de truite dans des conditions d'inhibition par l'ion mercurique, lorsque portées sur axe de probabilité vs le logarithme de la concentration d'ion mercurique, donnent une ligne droite. L'allantoïnase (EC 3.5.2.5) de *E. vancouveri* est inhibée par les cations bivalents de Cu, Hg, Zn, Pb et Cd. A de faibles concentrations ($\sim 10^{-8}$M), ces ions causent une augmentation d'activité de l'allantoïnase. Nous passons brièvement en revue l'adaptation des poissons à des changements dans l'environnement.

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ONE approach to the study of the effects of pollutants is through observations on the activity of enzymes in the presence of polluting substances. Already, much information on inhibitory effects of inorganic and organic substances on enzymes has been obtained (Hochster and Quastel 1963). Studies of enzyme inhibition complement those of in vivo bioassay procedures (Doudoroff et al. 1951; APHA et al. 1971). Enzyme assays performed in the presence and absence of a given pollutant can provide information on the nature and intensity of its effect and locus of action.

In our laboratory, we have for several years been examining the effects of various substances implicated in pollution on enzymes of aquatic organisms. In particular, we have inquired into the action of heavy metals on enzymes concerned with intermediary nitrogen metabolism. Heavy metals constitute a major source of pollution of our natural waters (Dyrssen et al. 1972), and nitrogenous substances such as proteins and nucleic acids are central components of living systems.

Techniques of tissue preparations and of assays for experiments described here are given in detail in the references cited. In general, homogenates of tissues are prepared which serve as the source of the enzyme to be studied. Portions of homogenates are incubated in the presence of substrate, buffer, cofactors, etc., and with or without the addition of the substance whose effect is to be tested. For detailed studies, an acetone-dried powder of a given tissue is prepared and stored at −18 C. The acetone-dried powder can also serve as the starting point for enzyme purification.

Mercury

The problem of mercury pollution has received much attention (Hartung and Dinman 1972; D'Itri 1972; Friberg and Vostal 1972). We (Wekell and Brown 1973) tested the effect of Hg^{2+} on the activity of rainbow trout (*Salmo*

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gairdneri) liver ornithine aminotransferase (EC 2.6.1.13) which catalyzes the reaction:

L-ornithine + α-ketoglutarate → L-glutamic-δ-semialdehyde + L-glutamate

This enzyme is closely related to those of the ornithine–urea cycle (Herzfeld and Knox 1968; Räihä and Kekomäki 1968; Sanada et al. 1970). It is also involved in the formation of the amino acid proline (Strecker 1957, 1960).

When the percentage inhibition of the trout liver enzyme by Hg^{2+} is plotted on a probability axis vs. Hg^{2+} concentration on a logarithmic axis, a straight line is obtained (Fig. 1). This plot indicates a log normal distribution as is found in most bioassay experiments with intact animals or their tissues. It permits an accurate determination to be made for the EC50 (effective concentration to yield 50% activity). The EC50 has the same meaning for enzyme inhibition as TL_m (median lethal tolerance) or LC50 (lethal concentration for 50% of test animals) have with experiments on intact animals. An EC50 inhibition value of 22×10^{-6}M Hg^{2+} (4.4 ppm) can be read from the graph of Fig. 1.

We find the EC50 value for Hg^{2+} to be dependent upon the state of purity of the enzyme tested, the EC50 inhibition value being lower the greater the purity of the enzyme. Hg^{2+} is known to form very strong complexes with sulfhydryl groups ($K_{dissoc} \sim 10^{-42}$; see Jocelyn 1972). Thus, there are apparently a number of nonspecific sites on proteins where Hg^{2+} is bound, reducing its effective concentration vis-à-vis inhibitory sites on the enzyme studied in the presence of other proteins. Investigators should be aware of this when attempting to extrapolate EC50 inhibition values obtained with enzymes to TL_m or LC50 values obtained with intact animals.

Mercuric ion also inhibits the enzyme allantoinase (EC 3.5.2.5) from the sabellid polychaete, *Eudistylia vancouveri* (May 1973). This enzyme catalyzes the reaction:

$$\text{allantoin} + H_2O \rightarrow \text{allantoic acid.}$$

The conversion of allantoin to allantoic acid is one step in the pathway for the breakdown of purines. In crude extracts an EC50 value of 70×10^{-6}M was found. Although the ultimate effects of Hg^{2+} on polychaetes is apparently unknown, inhibition of a step of a crucial degradative pathway in this polychaete would no doubt be of disadvantage to its economy. *Eudistylia vancouveri* and other sabellid worms feed on plankton (Fitzsimons 1965). Polychaetes in turn are fed on by fish and crabs (see May 1973). Until we know more of the flow of matter and energy in the marine environment, we cannot assess the ecological significance of mercury poisoning in polychaetes. We can only indicate that there exists a deleterious action of mercuric ion on at least one enzyme concerned with nitrogen metabolism in *E. vancouveri*.

Other Heavy Metals

While Hg^{2+} is inhibitory to polychaete allantoinase, Zn^{2+}, Pb^{2+}, and Cd^{2+} are even more so (Table 1). Surprisingly, allantoinase was found to be activated by very low concentrations of heavy metals (Table 2). This activation may be better described as an enhancing of enzymic activity above that achieved in the absence of very low concentrations of the metal ions.

Recently, James Webb in our laboratory found that Cd^{2+} at very low concentrations had an activating effect on glutamine synthetase (EC 6.3.1.2) from chinook salmon (*Oncorhynchus tshawytscha*) brain studied in the following assay system:

$$\text{glutamine} + NH_2OH + ADP \xrightarrow[HAsO_4^{2-}]{Mn^{2+}} \gamma\text{-glutamyl hydroxamate} + ADP + NH_3$$

In this assay for glutamine synthetase, Zn^{2+} and Cd^{2+} were shown to inhibit at concentrations $> 30 \times 10^{-6}$M (Webb and Brown 1975). But in the absence of Mn^{2+} we were surprised to find

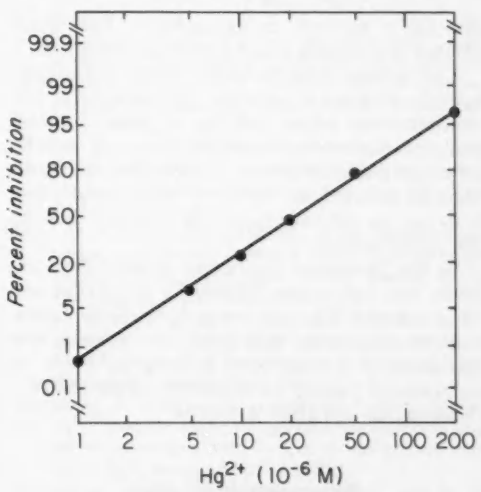

FIG. 1. Inhibition of partially purified ornithine aminotransferase from rainbow trout (*Salmo gairdneri*) liver by mercuric ion. Percentage inhibition (probability axis) vs. Hg^{2+} concentration (logarithmic axis). EC50 value for inhibition, 22×10^{-6}M. Plotted from data of Wekell and Brown (1973).

TABLE 1. Inhibition of allantoinase in *Eudistylia vancouveri* by heavy metals.[a]

Metal	EC50 (10^{-6} M)
Cu^{2+}	78
Hg^{2+}	70
Zn^{2+}	41
Pb^{2+}	35
Cd^{2+}	2.7

[a]Adapted from May (1973).

TABLE 2. Activation of allantoinase in *E. vancouveri* by "pollutant" heavy metals.[a]

Metal	Concn (10^{-8} M)	% activity
none		100
Hg^{2+}	17	120
Zn^{2+}	2.5	117
Pb^{2+}	2.5	117
Cu^{2+}	2.5	117
Cd^{2+}	2.5	110

[a]Adapted from May (1973); measurements were made in a complete assay system.

that Cd^{2+} restored partial activity. This phenomenon is currently under further investigation.

The findings show that some heavy metals may activate enzymes or enhance their activity at low concentrations while inhibiting at higher concentrations. Activation or enhancement of activity no doubt is a reflection of an evolutionary adjustment to background levels of heavy metals, that is to say, to naturally-occurring levels of these in the earth's waters.

In the glutamine synthetase assay, Mn^{2+} exhibits two values for EC50, 70×10^{-6}M and 11×10^{-3}M. The first value is for 50% activation, the second for 50% inhibition, showing that too much of a good thing is harmful. Mn^{2+} as an activator yielded its maximum effect (100%) between 300 and 1000×10^{-6}M.

Biogeochemical Cycles

These natural cycles are responsible for recycling elements between the biota, lithosphere, atmosphere and the hydrosphere. These cycles must take on the added burden of the cycling of man's increasing amounts of waste materials. With respect to "trace" metals (Pb, Cu, V, Ni, Cr, Sn, Hg, Cd), production of something of the order of 12 million metric tons/yr (National Academy of Sciences 1971) represents the added burden imposed on these cycles by man. As waste materials, the elements of this burden undergo processes of comminution, solution, precipitation, oxidation, reduction, complex formation, chelation, and adsorption, and they are subject at various stages to incorporation into biota with possible transfer and biomagnification through the food web to man. We need to have a better understanding of the permissible loading of these cycles by man's input and of the quantification of biotic transfer processes to properly assess man-made effects on the environment (see Schell and Barnes 1974).

In the meantime, studies on biochemical effects of "trace" and other heavy metals and of other pollutant chemicals, e.g. terphenyls, terephthalates, polychlorinated biphenyls, and other xenobiotics (Mason et al. 1965) can be conducted. This will aid in assessing specific effects of various chemicals currently or in the future disposed of or entering the earth's waters. Such studies will also aid in predicting what kinds of materials should be given special attention with respect to disposal methods.

For example, little is known about the effects of the rare earths on aquatic biota, although a number of these elements have been shown to inhibit several enzymes in mammals (principally) and some toxicity data are available (Haley 1965; Spassky 1974). With an increasing technology that involves the use of "exotic" elements in a number of industrial devices (MacLean 1975), we would do well to make inquiries into the effects of such elements on the metabolism of a variety of aquatic organisms. The final disposal of such devices will increase the concentrations of these elements in our waters.

Adaptation to Environmental Insults

There is little in the literature concerning biochemical strategies dealing with increased levels of heavy metals in our waters. However, the studies of Margoshes and Vallee (1957) indicate that a specific inducible (Winge and Rajagopalan 1972) protein (or group of proteins termed metallothioneins) occurs in vertebrates, including fish (R. W. Olafson personal communication), that binds heavy metals. This protein(s) is rich in the sulfhydryl-containing amino acid cysteine, accounting for its scavenging of heavy metal cations.

Recently, in our laboratory Mary Lou Mills (1975) found a very steep bioassay curve for Cr^{3+} with yearling coho salmon (*O. kisutch*).

This suggests that these fish tolerate Cr^{3+} up to a given concentration by actively secreting it back into the water (by gills or kidney) or by having it bound to a specific protein. But once a threshhold value is reached, only a slightly higher concentration causes 100% mortality. This threshhold concentration for yearling coho salmon in sea water precedes the narrow range of 48–52 ppm Cr^{3+} for 1–99% mortality.

Organic pollutants are handled by organisms by enzymic detoxification processes. Aryl compounds have been shown to undergo hydroxylation by the P_{450} cytochrome oxidase of trout liver (Pederson et al. 1974). The trout enzyme is inducible, suggesting that when confronted with an increased level of organic pollutant, fish have a genetic reserve of detoxifying ability. The finding by Somero and Hochachka (1971) that, under temperature stress, rainbow trout (*S. gairdneri*) develop new and advantageous isozymic patterns, affords us the opportunity of viewing the dynamic aspects of resistance to stress by fish under changing environmental conditions.

Recently Johnston (1975) found that carp (*Cyprinus carpio*) perform a fermentation of glucose to L-alanine and succinate in red muscle when under anaerobic conditions. This enables an extra ATP to be formed under anaerobiosis which is not available with the usual lactic acid as end product.

Conclusion

I have provided some examples from our laboratory on the use of enzymes for describing the effects of heavy metals on aquatic organisms. All the natural elements are found at some concentration in our natural waters. But it is the increasing concentration of these, owing to man's activities, that poses problems. Also, I cited some examples from the work of other laboratories to indicate various biochemical tools possessed by biota that aid in dealing with possible stresses imposed on them by man's introduction of his wastes into the environment. A continuing study of metabolic and enzymic activities of aquatic organisms is essential to provide us with a rational basis for anticipating and understanding the ecological effects of an accelerated input or additions of new chemicals into the freshwater and marine environments.

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Effects of Copper or Zinc in Fresh Water on the Adaptation to Sea Water and ATPase Activity, and the Effects of Copper on Migratory Disposition of Coho Salmon (*Oncorhynchus kisutch*)[1]

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LORZ, H. W., AND B. P. MCPHERSON. 1976. Effects of copper or zinc in fresh water on the adaptation to sea water and ATPase activity, and the effects of copper on migratory disposition of coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 2023–2030.

The 96-h LC50 of copper ($CuCl_2$) for yearling coho salmon (*Oncorhynchus kisutch*) was found to decrease from 74 μg/liter Cu in November to 60 μg/liter in May as the fish became smolts. The 96-h LC50 of zinc ($ZnCl_2$) for yearling coho in April was 4600 μg/liter Zn. All tests were conducted at 10–12 C in water with alkalinity and hardness ranging from 68 to 78 and 89 to 99 mg/liter as $CaCO_3$, respectively.

Exposures of yearling coho for 144 h to sublethal concentrations of zinc in fresh water had little effect on the enzyme activity of Na^+, K^+-activated ATPase in gill microsomes or on the survival of fish transferred to sea water. Acute and chronic exposures (maximum of 4128 h) of yearling coho salmon to sublethal concentrations of copper (5–30 μg/liter) in fresh water had deleterious effects on downstream migration after the fish were placed in a natural stream, gill ATPase activity, and survival in sea water. More severe effects were produced in the chronic exposures than in 144-h exposures on downstream migration and survival in sea water, but not on gill ATPase. Effects of copper began to occur within 24–72 h and were often maximized within 120–144 h of exposure. Concentrations of copper (5–20 μg/liter) were 0.09–0.35 of the 96-h LC50 for coho smolts.

LORZ, H. W., AND B. P. MCPHERSON. 1976. Effects of copper or zinc in fresh water on the adaptation to sea water and ATPase activity, and the effects of copper on migratory disposition of coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 2023–2030.

La CL50 après 96 h du cuivre ($CuCl_2$) pour des saumons coho (*Oncorhynchus kisutch*) de l'année diminue de 74 μg/litre de Cu en novembre à 60 μg/litre en mai au moment où les poissons se transforment en smolts. La CL50 après 96 h de zinc ($ZnCl_2$) pour des saumons coho de l'année en avril est de 4600 μg/litre de Zn. Tous les essais ont été effectués à 10–12 C, dans de l'eau d'alcalinité et de dureté allant de 68–78 et 89–99 mg/litre de $CaCO_3$ respectivement.

Des expositions de saumons coho de l'année durant 144 h à des concentrations sublétales de zinc en eau douce ont peu d'effet sur l'activité enzymique de l'ATPase activée au Na^+ et au K^+ dans les microsomes branchiaux, ou sur la survie de poissons transférés dans l'eau de mer. Des expositions aiguës et chroniques (maximum de 4128 h) de saumons coho de l'année à des concentrations sublétales de cuivre (5–30 μg/litre) en eau douce ont des effets nuisibles sur la migration d'avalaison une fois les poissons placés dans un cours d'eau naturel, de même que sur l'activité de l'ATPase branchiale et sur la survie dans l'eau de mer. Les expositions chroniques ont des effets plus graves que les expositions de 144 h sur la migration d'avalaison et sur la survie en eau de mer, mais non sur l'ATPase branchiale. Les effets du cuivre commencent à se faire sentir en dedans de 24–72 h et atteignent souvent un maximum en dedans de 120–144 h d'exposition. Les concentrations de cuivre (5–20 μg/litre) sont de 0.09–0.35 de la CL50 après 96 h pour les smolts de saumon coho.

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THE seaward migration of juvenile coho salmon (*Oncorhynchus kisutch*) normally occurs during the spring of their second year of life. They are euryhaline several months earlier provided that they achieve a threshold size of 9 cm (Conte et al. 1966). The natural movement or experimental transfer of juvenile anadromous salmonids from fresh water to sea water is followed by a transient but marked disturbance of water–electrolyte balance (Conte et al. 1966; Miles and Smith 1968).

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These disturbances are minimized at the time of normal seaward migration or "parr–smolt transformation."

One of the physiological factors correlated with migratory behavior in steelhead trout (*Salmo gairdneri*) is an elevation of activity in Na^+, K^+-stimulated adenosine triphosphatase (ATPase) in gill microsomes (Zaugg and Wagner 1973). This enzyme activity increases twofold during parr–smolt transformation of coho salmon and steelhead trout (Zaugg and McLain 1970, 1972; Zaugg and Wagner 1973). Activity in salmonids and other euryhaline fishes continues to increase after the first few days in sea water, reaching a maximum after about 30 days, and is thought to be important in maintaining their salt and water balance (Epstein et al. 1967; Zaugg and McLain 1970).

Considerable research has been done to determine the effects of copper or zinc on the survival and growth of juvenile salmonids in fresh water (Chapman 1973; Hodson and Sprague 1975; Lloyd 1960; McKim and Benoit 1971; Sprague 1964; Sprague and Ramsay 1965). However, there is a paucity of information available for establishing water quality criteria as they relate to the migration of fish into sea water following toxicant exposure. There is a particular need for this type of data in the Pacific northwest where large runs of anadromous salmonids are a valuable sport and commercial fishery resource and whose well-being is a significant factor in environmental impact considerations. This study was designed to determine the effects of copper or zinc (in fresh water) on yearling coho salmon's ability to adapt to sea water, ATPase activity, and effects of copper on downstream migration.

Materials and Methods

Experimental Fish

Coho salmon of the 1972 and 1973 year-classes from Fall Creek Salmon Hatchery (Alsea River, Oregon) were used. Fertilized eggs were incubated at temperatures that ranged from 7.8 to 12.3 C. The fish were reared under natural light or simulated natural photoperiod in well water at a constant temperature of 12.3 C. In 1974 the experimental fish (1972 brood year) were reared and tested at a constant temperature (12.3 C). In 1975 the experimental fish (1973 brood year) were reared and exposed to toxicant at 12.3 C until February 1. Fish were then acclimated to 8.6 C over a 6-day period and exposed to a simulated natural temperature; 8.6 C on February 7 to 12.3 C on May 19. The temperature pattern used was based on mean biweekly maximal and minimal temperatures for the North Fork of the Alsea River.

Fish were fed a commercially prepared moist pellet generally to repletion. Fish were not fed during the 24 h preceding exposures to toxicant, during acute ($\leqslant$144 h) toxicant experiments, nor during exposures to sea water. Feeding of fish was resumed in the chronic experiments after the first 144 h.

Exposures to Toxicant

All exposures were conducted on coho salmon between the ages of 10 and 18 mo posthatching. Fish were exposed to copper ($CuCl_2$) for periods ranging from 24 to 4128 h. Four 144-h exposure tests were also conducted with zinc ($ZnCl_2$). All 96-h LC50s were determined from static water bioassays in 61-cm diam fiberglass tanks. The water was continuously aerated and 85% of the 120 liters of test water was exchanged daily. Toxicant solutions were mixed in a separate container prior to introduction to the tanks. Total metal concentrations in daily water samples were assayed by atomic absorption spectrophotometry. Loss of metal from the test water during any 24-h period was undetectable. The tanks were maintained at 12 $\pm$ 1 C in 1974 and 10 $\pm$ 1 C in 1975, with simulated natural photoperiod. The above procedure was used for the static 144-h copper exposures in 1974, and all zinc exposures.

Exposures of more than 144 h, as well as some $\leqslant$144 h, were conducted in a flowing water system. This system consisted of a gravity flow dilutor that delivered 12 liters/min to each exposure tank. Nominal concentrations of copper were 30, 20, 10, 5 and 0 μg/liter and were duplicated. The background concentration of copper in the well water was less than 2 μg/liter. A volume of 1000 liters was maintained in each of the ten 1.5-m diam fiberglass tanks. At the measured flow rate, 99% of the water was replaced every 5.5 h. A submersible pump was used in each tank to provide additional mixing.

Smaller groups of "stock" fish were exposed to the flowing toxicant in 61-cm diam fiberglass tanks to provide test fish with shorter toxicant exposures. Flows to these 120-liter tanks were provided by siphons from mid-depth in the 1.5-m tanks, with no change in water quality observed. All tanks were covered with nets to prevent loss of fish. In 1975 a curtain was installed around the periphery of the tanks to minimize disturbance from external sources.

Concentrations of copper used were chosen on the basis of prior static water bioassays. Total copper concentration was analyzed at least once per week in water from each exposure tank by atomic absorption spectrophotometry. Water and toxicant flows in the dilutor were checked at least once daily. Only minor adjustments were required. Nominal concentrations of toxicant will be used in the Results and Discussion since measured concentrations were within $\pm$10% of these values. A summary of routinely measured water quality is listed in Table 1.

Tolerance to Sea Water

Tests of tolerance to sea water were conducted on samples of 10–20 fish from each toxicant exposure tank. Survival was used as a measure of osmoregulatory ability. Fish were placed into the 61-cm diam

TABLE 1. Range of values for water quality assays in test tanks during exposures to toxicant.

Parameter and units	Exposure system	
	Static	Flowing
Dissolved oxygen: mg/liter	6.0–10.8	7.3–10.5
Alkalinity: mg/liter $CaCO_3$	68–78	72–75
EDTA hardness: mg/liter $CaCO_3$	89–99	84–99
pH	6.8–7.9[a]	7.2–7.5
Total ammonia: mg/liter NH_3-N	0.04–0.44[a]	0.12–0.57

[a]Reflects diel fluctuations caused by daily exchange of 85% of the water in the test tanks.

fiberglass tanks containing 120 liters of natural sea water. Salinity of the water ranged from 29 to 33‰ in 1974 but was maintained at 30.0 ± 0.5‰ in 1975. The tanks were maintained at 12 ± 1 C in 1974 and 10 ± 1 C in 1975, under simulated natural photoperiod. The seawater exposure period was 15–20 days in 1974 but was reduced to 10 days in 1975 because all deaths usually occurred before the eighth day.

During the tests in sea water, dissolved oxygen in the water was maintained at 6.4–8.5 mg/liter and pH at 7.4–8.1. The total ammonia ranged from 0.04 to 1.8 mg/liter NH_3-N due to the daily exchange of 85% of the water in the test tanks.

DOWNSTREAM MIGRATION

Effects of copper on migration were assessed by releasing fish into a tributary to the North Fork of the Alsea River and enumerating migrants entering a trap 6.4 km downstream. The trap was built into a permanent weir and usually was checked daily. On the day prior to release, 50–100 fish from each copper test tank were anesthetized with MS-222®, weighed, measured, and identified by freeze branding and fin-excision. Parr–smolt transformation is markedly size dependent and seasonal in this stock. Wild coho juveniles normally spend 1 yr in the natural stream before migrating seaward provided they have reached the size of 7 cm. Under artificial propagation most fish reach a size of 11–15 cm in less than 1 yr. No fish less than 10 cm were released. Seaward migration normally begins in April, peaks in late May, and ceases by late June. Releases of copper intoxicated fish and their controls were made between April 8 and June 4, 1975. trapping was terminated in early July, 1 mo after the last release.

GILL ATPASE ACTIVITY

The activity of Na^+, K^+-activated ATPase in microsomes isolated from gill filaments was assayed by the procedures of Zaugg and McLain (1970). The activity was measured in three to six fish per toxicant concentration prior to release into the stream and before most tests in sea water. Enzyme assays were also made from gill tissues of survivors of two tests in sea water.

No inhibition of the ATPase activity occurred when $CuCl_2$ was added to homogenized gill tissue from control fish. Final concentrations of copper in the spiked homogenates (0.04 gm of tissue/ml of homogenate) were up to 10 μg/ml Cu, which was over 200 times the concentration found in the gills of coho salmon exposed to 30 μg/liter Cu in fresh water. This suggests that the decreased ATPase activity observed in gills from fish exposed to copper was not a result of copper ions liberated during the homogenization procedure. Free copper ions are probably bound by the EDTA (5mM) in the homogenizing solution (W. S. Zaugg unpublished data).

Results and Discussion

In the first 20 mo of study, six static water bioassays of copper and four of zinc were completed. In addition, 16 tests of tolerance to sea water were run using fish exposed to copper in the flowing toxicant system. Only a few of the tests will be discussed.

96-H LC50 EXPERIMENTS

The 96-h LC50 of copper for juvenile coho salmon was determined at 3 different times. In late November it was 74, in early March it was 70, and by late May it dropped to 60 μg/liter Cu. The greater sensitivity to acutely lethal effects of copper in May was probably due to the onset of smoltification rather than increasing age or size of fish. This physiological transformation, which preadapts coho salmon to a seawater existence, apparently increased their susceptibility to lethal effects of copper in fresh water. The observed increase may have been modified slightly in either direction because the earlier tests were conducted at a higher temperature (12 C) than the May test (10 C) and the interactions between temperature and metal toxicity are complex (Hodson and Sprague 1975). Water hardness, alkalinity, pH, ammonia, and dissolved oxygen values were similar in all tests.

Our 96-h LC50 values of copper for coho

TABLE 2. Survival and gill ATPase activity of yearling coho salmon (*Oncorhynchus kisutch*) exposed to copper in static fresh water and their subsequent survival, and gill ATPase activity after transfer to sea water.

Nominal concn (*μg/liter Cu*)	% Survival in toxicant (*144-h exposure*)[a]	ATPase activity in toxicant[b]	% Survival in sea water	ATPase activity in sea water[b]
		Mar. 20–Apr. 8, 1974[c]		
0	100	12.9	94	51.4
20	100	7.1	6	63.4[d]
30	100	5.6	0	
50	95	5.0	0	
60	85	—	0	
80	25	—	0	
		Apr. 16–May 6, 1974[e]		
0	100	25.5	100	57.3
5	100	16.3[f]	94	58.6
10	100	9.8[f]	59	57.8
20	100	6.6[f]	24	53.7[f]
30	100	6.5[f]	6	70.2[d]
60	30	4.0[g]	0	

[a]Twenty fish exposed per concentration.
[b]Gill microsomal Na^+, K^+-activated ATPase; micromoles ATP hydrolyzed per milligram protein per hour; mean of four fish at the end of exposure.
[c]312-h seawater exposure.
[d]Only one fish.
[e]336-h seawater exposure.
[f]Mean of three fish.
[g]Mean of two fish.

salmon are higher than those reported by Sprague (1964) for Atlantic salmon (*S. salar*) and Lloyd and Herbert (1962) for rainbow trout (*S. gairdneri*). However, the alkalinity and hardness of our water (66 and 95 mg/liter $CaCO_3$, respectively) were about 4 times greater, and our fish were larger and of a different genus than those used in the cited studies. Chapman (unpublished data) found that the 96-h LC50 of copper for juvenile coho salmon (same stock as used in our studies) was 28–38 μg/liter Cu at the Western Fish Toxicological Station, Corvallis, Oregon, with a water hardness and alkalinity of 20–25 mg/liter $CaCO_3$.

The 96-h LC50 of zinc for yearling coho salmon was 4600 μg/liter in April at 12 C. Our 96-h LC50 value for zinc is higher than that reported by other investigators for salmonids (Chapman 1973; Hodson and Sprague 1975; Sprague 1964). However, the greater alkalinity and hardness of the water in our studies may account for the difference.

SURVIVAL IN SEA WATER AND GILL ATPASE

The survival and gill microsomal Na^+, K^+-activated ATPase activity of yearling coho salmon exposed to copper for 144 h in static fresh water and their survival following transfer to sea water in two 1974 tests is presented in Table 2. The ATPase activity in fresh water and the percent survival in sea water were decreased in proportion to the concentration of copper. The decreased ATPase activity probably was one of the factors leading to loss of osmoregulatory ability and death in sea water. The ATPase activity in fish that survived exposure to sea water for 312 h was increased two- to threefold over the values obtained for coho in fresh water, corroborating the results of Zaugg and McLain (1970).

Exposures of yearling coho for 144 h to sublethal levels of zinc in static fresh water ($\leqslant$2000 μg/liter) did not seriously affect subsequent survival in sea water (Table 3). The percent survival in sea water was not consistently related to the zinc concentrations, reflecting the tendency of fish to become hypersensitive and hyperactive to stimuli during and after exposures of $\geqslant$1000 μg/liter Zn. These responses were quite variable and were sometimes followed by tetanic spasms and death of the fish.

Gill microsomal Na^+, K^+-activated ATPase activity appears unaffected by zinc (Table 3). The apparent stimulation in the March test is probably an artifact of the fish analyzed as controls as these fish were subjected to a low copper

TABLE 3. Survival and gill ATPase activity of yearling coho exposed to zinc in static fresh water and their subsequent survival, and gill ATPase activity after transfer to sea water.

Nominal concn (*μg/liter Zn*)	% Survival in toxicant (*144-h exposure*)[a]	ATPase activity in toxicant[b]	% Survival in sea water	ATPase activity in sea water[b]
		Mar. 20–Apr. 8, 1974[c]		
0	100	12.9[d]	100	51.4
100	100	22.2	94	70.1
300	100	—	100	65.7
600	100	26.6	100	76.9
1000	100	24.4	81	95.0
2000	100	29.8	81	70.5
2500	100	25.8	87	66.2
		Apr. 16–May 6, 1974[e]		
0	100	25.5[f]	100	57.3
2500	85	21.6[f]	100	48.6[f]
4000	75	21.8[f]	67	46.5[f]
5000	65	20.2[f]	80	58.3[f]
6000	10	—	50	—

[a]Twenty fish exposed per concentration.
[b]Gill microsomal Na^+, K^+-activated ATPase; micromoles ATP hydrolyzed per milligram protein per hour; mean of four fish at the end of exposure.
[c]312-h seawater exposure.
[d]Control also served for copper exposed fish concurrently being run (see Table 2).
[e]336-h seawater exposure.
[f]Mean of three fish.

TABLE 4. Gill ATPase activity and survival in sea water of yearling coho exposed to copper in fresh water for ≤144 h (tests conducted from March 6 to June 9, 1975). Number of fish is in parentheses.

Nominal concn (*μg/liter Cu*)	Exposure time (*h*)	ATPase activity in toxicant (*mean* ± SD)[a]	% Survival in sea water (*240–312-h exposure*)
0	144	46.3±8.8 (18)	100.0 (103)
10	144	39.3±8.0 (4)	98.8 (83)
20	144	—	60.7 (107)
30	144	13.4±3.1 (8)	10.1 (99)
30	120	15.4±1.5 (4)	9.5 (21)
30	96	17.2±4.6 (4)	45.0 (20)
30	69	—	61.0 (59)
30	56	30.2±13.5 (4)	—
30	41	—	78.0 (41)
30	24	—	75.6 (41)

[a]Gill microsomal Na^+, K^+-activated ATPase; micromoles ATP hydrolyzed per milligram protein per hour.

contamination (13.7 μg/liter). The acute toxicity of zinc to yearling coho salmon appears to involve a different mechanism than that of copper, as indicated by the difference in effects of the two metals on gill ATPase and subsequent survival in sea water.

Yearling coho salmon subjected to 30 μg/liter Cu in fresh water for only 24 h suffered a 25% mortality upon transfer to sea water (Table 4). The number of deaths in sea water increased with longer exposures to toxicant but reached a maximum at 96–120 h of copper exposure (Table 4). Inhibition of gill ATPase was also observed in these exposures (30 μg/liter Cu), although data on exposures of less than 56 h were not obtained.

The effects of copper on seawater tolerance

were greater after exposures to toxicant in the static water system (Table 2) than after exposures in the flowing water system (Table 4). This was probably due to the manual water changes (once per day) which caused greater excitation of the fish and fluctuations in water chemistry (Table 1) during the static exposures. The values for gill ATPase activity in Table 2 (1974) are lower than those in Table 4 (1975) but probably do not represent biological differences. The discrepancies may be due partially to the use of a different centrifuge for enzyme isolation in 1975.

The survival of juvenile coho salmon in sea water following exposure to copper in fresh water for 144 h at different times of the year is shown in Fig. 1. The effects were dependent upon copper concentration during tests on any given date, but there was a trend toward reduced effect with the onset of smoltification in the fish. Disturbance of osmotic balance in the fish upon transfer to sea water is minimized during smolting process (Conte et al. 1966). This physiological process reduced the deleterious effects of copper on survival of smolts in sea water, although increasing size and age may have helped.

In June to early August 1974, four survival tests in sea water were run on coho salmon from the flowing toxicant system after 144–880 h of copper exposure. From mid-December to early June 1975, five survival tests in sea water were carried out with coho salmon exposed to copper from 144 to 4128 h. Data showing the survival in sea water of exposure groups in 1975 are shown in Fig. 2. A noticeable increase in tolerance to sea water was seen as the season progressed, very similar to the pattern observed for coho salmon exposed for only 144 h (Fig. 1). However, the chronically exposed fish generally had less tolerance for sea water than did the 144-h exposed fish. This was due partly to poorer condition and

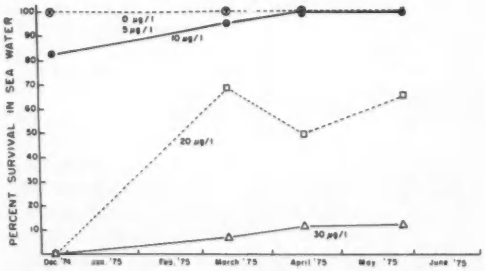

Fig 1. Survival of juvenile coho (*Oncorhynchus kisutch*) in sea water following exposure to copper in fresh water for 144 h at different times of the year (each point represents 16–45 fish).

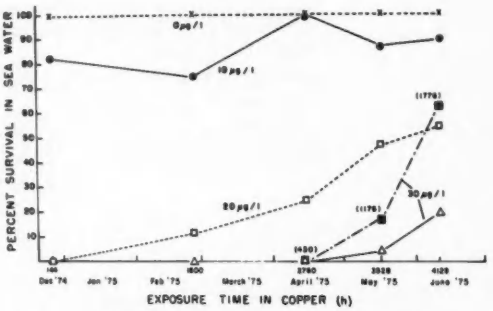

FIG. 2. Survival of juvenile coho in sea water at different times of the year following exposure to copper in fresh water starting on December 20, 1974 (each point represents 20–45 fish). Numbers in parentheses indicate exposure hours of an additional group of fish placed in copper on March 27, 1975 (first two points represent 40 fish, last point represents 11 fish).

nutritional state and smaller size of the chronically exposed fish resulting from a suppression of feeding in the copper toxicant, in a concentration dependent manner. These same factors precipitated an earlier onset of mortality in sea water (Fig. 3B).

A marked recovery of ability to survive in sea water during May and June was observed in the survivors of groups chronically exposed to 30 µg/liter Cu (Fig. 2). The fish that remained were copper-resistant and subsequently began to recover their appetite. Recovery of feeding improved their condition and nutritional state, and consequently improved their tolerance for sea water. In both groups chronically exposed to 30 µg/liter Cu, recovery of feeding responses began to occur in May, although one group had been exposed for over 3500 h and the other for less than 1200 h. Therefore, during the April, May, and June tests of survival in sea water, fish in the group exposed for the shorter time to copper were larger and in better condition as well as having begun parr–smolt transformation before their exposure to copper started on March 27. It must be a combination of these factors that resulted in the quicker and greater recovery of tolerance to sea water in this group.

No deaths occurred during the 144-h freshwater copper exposures (Fig. 3A) but upon transfer to sea water the coho previously exposed to 20 and 30 µg/liter began to die following 72 h in sea water. In the chronically exposed groups deaths in the 30µg/liter Cu (freshwater) began to occur after 144 h of exposure and reached an asymptote after 1800 h (Fig. 3B). Coho salmon yearlings, previously exposed to 20 and 30 µg/

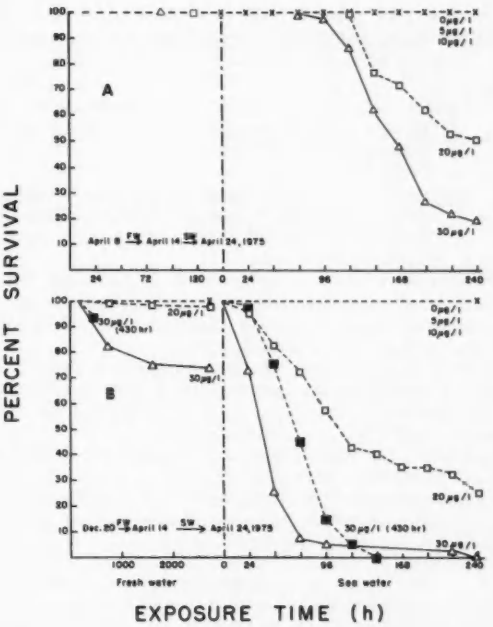

FIG. 3. Survival curves of yearling coho during exposures to copper in fresh water and subsequent seawater exposure in April. A, Copper exposure for 144 h and then transferred to sea water for 240 h; B, Copper exposure of 2760 h (also includes a group exposed to 30 μg/liter for 430 h) and then transferred to sea water for 240 h.

liter Cu for over 2700 h, began to die within 12 h following transfer to sea water (Fig. 3B). This lower tolerance for sea water of the chronically exposed fish is due partially to their poorer condition.

The gill microsomal Na^+, K^+-activated ATPase activity of juvenile coho salmon chronically exposed to copper starting on December 20, 1974 is shown in Fig. 4. A peak in activity occurred in the control fish during April and May, corroborating the data of Zaugg and McLain (1970). Gill ATPase activity was suppressed by copper, but did not reflect the increasing tolerance of coho salmon to sea water that occurred as the season progressed (Fig. 2). This lack of correlation and the large variability in activity levels between fish in the same group limits the use of gill ATPase activity as an indicator of tolerance.

Downstream Migration

Four releases of coho salmon exposed to copper since late December and two releases of coho exposed to copper for 144 h were made into

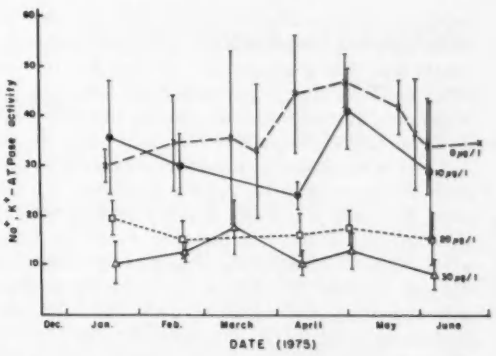

FIG. 4. Influence of exposure to copper in fresh water on gill microsomal Na^+, K^+-activated ATPase activity of juvenile coho chronically exposed to copper starting on December 20, 1974. Each point represents four to six fish (micromoles ATP hydrolyzed per milligram protein per hour ± SD).

Crooked Creek, a tributary of the Alsea River. The releases were made from early April to June 1975, during the normal migration period. The control fish showed the best movement with fewer fish migrating with increasing copper concentration (Fig. 5). Similar trends of movement occurred in the various exposure groups released earlier. Even the lowest concentration used (5 μg/liter), which had no measurable effect on gill ATPase activity or survival in sea water in the 1975 experiments, reduced the percentage of downstream migrants. As noted in the seawater tolerance tests, survivors of a group chronically exposed to 30 μg/liter (initiated March 27) had recovered some of their migrational abilities as the season progressed (Fig. 5).

A greater percentage of fish from the 144-h

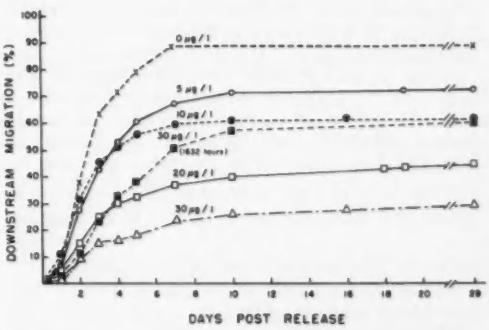

FIG. 5. Influence of exposure to copper for 3960 h in fresh water on percent downstream migration of yearling coho (includes coho exposed to 30 μg/liter Cu for 1632 h). Each line represents 78–172 fish released on June 4, 1975.

exposure groups migrated than did the chronically copper exposed fish at each respective concentration. Exposure to 30 μg/liter Cu for as little as 72 h caused a considerable reduction in migration as compared to control fish (52 and 93% movement, respectively).

Most of the fish that moved downstream to the weir did so within the 1st wk following release (Fig. 5). Only a few fish showed delayed migration arriving at the trap between 8 and 29 days after release. A large percentage of the fish that did not migrate by early July, including control fish, are presumed to have died. In migration studies in prior years, electrofishing the stream above the weir following the normal migrational period accounted for 5% or less of the fish that did not migrate.

These results indicate that concentrations of copper that were sublethal to yearling coho salmon in fresh water reduced the chances of successful migration to the ocean and adaptation to sea water. These concentrations (5–20 μg/liter Cu) were 0.09–0.35 of the 96-h LC50 of copper for coho salmon during their normal seaward migration in May. Direct effects of copper on ATPase activity and adaptation to sea water began to occur within 24–72 h and were maximized within 120–144 h. Secondary effects related to suppression of appetite in the copper toxicant magnified the effects on downstream migration and adaptation to sea water in exposures >144 h.

Acknowledgments

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Progress in Sublethal Effect Studies with Kraft Pulpmill Effluent and Salmonids[1]

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DAVIS, J. C. 1976. Progress in sublethal effect studies with kraft pulpmill effluent and salmonids. J. Fish. Res. Board Can. 33: 2031–2035.

Literature values of incipient sublethal response threshold concentrations for salmonids to effluent from neutralized whole bleached kraft mills, kraft bleaching, and the production of unbleached pulp for salmonids are summarized. Sublethal responses include effects on growth, behavior, energetics, metabolism, respiration, circulation, and temperature tolerance in a variety of salmonids. The average incipient threshold concentration for all species surveyed was 0.16 of the 96-h LC50 and ranged from 0.006 to 0.33 96-h LC50 for neutralized whole bleached kraft mill effluent. Large differences in sensitivity were not evident between salmonid species or the three effluent types surveyed.

On the basis of this analysis, I suggest for neutralized whole bleached kraft mill effluent, that some sublethal effects will be present at a discharge dilution of 0.1 96-h LC50, few at 0.05 96-h LC50, and only rarely at 0.02 96-h LC50. However, at a dilution of 0.02 of the 96-h LC50, flesh tainting or color effects on the food chain may remain. These criteria are considered tentative and subject to revision with new knowledge and do not necessarily ensure protection of aquatic communities or sensitive food-chain organisms.

Future research needs and suggestions for criteria implementation are discussed.

DAVIS, J. C. 1976. Progress in sublethal effect studies with kraft pulpmill effluent and salmonids. J. Fish. Res. Board Can. 33: 2031–2035.

L'auteur résume les valeurs publiées des concentrations de seuil déclenchant une réponse sublétale chez les salmonidés exposés à des eaux usées entières neutralisées de blanchiment de papeterie kraft, de blanchiment de papier kraft et de pâte non blanchie. Les réponses sublétales comprennent des effets sur la croissance, le comportement, l'énergétique, le métabolisme, la respiration, la circulation et la tolérance à la température chez une variété de salmonidés. La concentration de seuil moyenne de début de réponse pour toutes les espèces étudiées est de 0.16 de la CL50 après 96 h. Pour l'effluent blanchi entier neutralisé de papeterie kraft, cette valeur varie entre 0.006 et 0.33 de la CL50 après 96 h. L'auteur n'a pas décelé de grandes différences de sensibilité entre les espèces de salmonidés ou entre les trois types d'eaux usées étudiées.

Sur la base de cette analyse, l'auteur suggère que, dans le cas d'eaux usées blanchies entières neutralisées de papeterie kraft, il y aura des effets sublétaux à une dilution d'effluent de 0.1 de la CL50 après 96 h, peu d'effets à 0.05 de la CL50 après 96 h et de rares effets seulement à 0.02 de la CL50 après 96 h. A une dilution de 0.02 de la CL50 après 96 h, cependant, la coloration de la chair ou des effets de coloration sur la chaîne alimentaire persistent. Nous considérons ces critères comme provisoires et sujets à révision avec l'acquisition de nouvelles connaissances; ils n'assurent pas nécessairement une protection aux communautés aquatiques ou aux organismes sensibles de la chaîne alimentaire.

L'auteur discute des besoins futurs en recherches et de suggestions sur l'application de ces critères.

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IN Canada large volumes of kraft pulpmill waste are discharged into freshwater, marine, and estuarine areas, posing a potential pollution threat to aquatic life. This waste, termed kraft mill effluent (KME), results from digestion of wood in an alkaline mixture of sodium salts, frequently followed by bleaching to achieve brightness in the pulp.

Considerable effort has been devoted to acute fish toxicity studies with KME (Alderdice and Brett 1957; Betts and Wilson 1967; Hicks and DeWitt 1971; Howard and Walden 1965, 1971, 1972; Servizi et al. 1966; Servizi and Gordon 1973; Sprague and McLeese, 1968a, b; Werner 1963). Only recently however, has considerable effort been devoted to sublethal effect studies

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with KME and fish. Such work has been devoted almost exclusively to salmonid studies. It is important that sublethal effect studies identify incipient threshold concentrations where long-term responses just begin to appear so that such concentrations can be incorporated into receiving-water criteria for protection of fish populations. The purpose of this paper is to summarize progress to date, identify the nature of sublethal responses described, and arrive at tentative recommendations for receiving-water criteria. The analysis is confined to salmonids frequenting Canadian waters as information on other species' sensitivity to KME is scarce.

Effluent from the Kraft Process

Kraft pulpmills are highly complex and frequently differ widely in layout and process from mill to mill. Variations occur in the mixture of chemicals used in pulping, the bleach sequence and nature of bleaching, wood furnish used, degree of recycling of chemicals, and treatment practiced, between mills and within a given mill with time. For these reasons, comparison of test results from the literature is difficult and open to criticism. This report deals with responses of salmonids to composite, neutralized whole bleached kraft mill waste, to bleach plant waste, and to waste from production of unbleached pulp.

Sublethal Effects of Whole Kraft Mill Waste

Table 1 summarizes sublethal effects reported for different salmonid species by various workers. Effects are evident in growth, behavior, swimming energetics, respiration, temperature tolerance, circulation, and metabolism of salmon. For all species the average sublethal concentration threshold is 0.16 of 96-h LC50 and ranges from .006 to 0.33 of the 96-h LC50. The more sensitive sublethal thresholds appear to involve behavior, temperature tolerance, and cough frequency. Growth retardation and enhancement are reported, suggesting that growth may not be a reliable and easily interpreted response for test purposes. No large differences in salmonid species' sensitivity are apparent in Table 1. In addition, long-term tests of up to 200 days appear to yield no more sensitivity than short-term tests spanning a few hours.

Sublethal Effects of Unbleached Kraft Effluent and Bleach Plant Effluent

Table 2 summarizes results obtained in tests with neutralized bleach plant waste and unbleached waste. Much less work has been done with these wastes than with whole bleached kraft mill effluent; however, sublethal threshold values appear similar to those for whole mill effluent. Aberrancies in growth and behavior are evident in Table 2. Averaging the sublethal response concentrations for neutralized kraft mill bleach plant waste yields a mean of 0.375 of the 96-h LC50 and range of 0.05–0.8 of the 96-h LC50. Obviously, more data are required to define the average sublethal threshold concentration more precisely for both waste types.

Isolated Toxic Components

Recently, considerable effort has been devoted to identifying persistent organic toxic components of KME that are likely to be hazardous to fish. Major toxic organic components isolated from whole kraft mill effluent include resins acids, polyunsaturated fatty acids (Leach and Thakore 1973; Maenpaa et al. 1968; Rogers 1973; Rogers and Mahood 1974) and in mills pulping lodgepole pine, a mixture of diterpene alcohols and aldehydes closely related structurally to resin acids (Rogers and Mahood 1974). This mixture of diterpene alcohols and aldehydes appears in a toxic neutral (unsaponifiable) fraction from waste originating during the pulping of lodgepole pine (Rogers et al. 1975). Part of this toxic neutral fraction also appears in waste from the pulping of other species such as Douglas fir.

So far, relatively little is known of the sublethal effects of these toxic components on fish. Resin acids appear to enter the body of fish, probably via the gills, and accumulate in liver, kidney, and brain tissue during static bioassays (G. M. Kruzynski personal communication). Field experiments have demonstrated widespread histological damage to the fish *Sparus macrocephalus* in Japanese waters (Fujiya 1961, 1964); however, such histological damage has not been reported for fish exposed to effluent from North American mills. Chlorinated organics such as the catechols and guaiacols are known to be present in effluents (Rogers and Keith 1975) and resemble the structure of pentachlorophenol, an uncoupler of oxidative phosphorylation. Servizi et al. (1968) reported elevated respiration rates in sockeye salmon (*Oncorhynchus nerka*) fry exposed to 0.1 mg/liter tetrachlorcatechol, possibly indicating disruption of oxidative phosphorylation. Kruzynski (personal communication) demonstrated that the acute toxicity of dehydroabietic acid, a resin acid, was considerably less in sea water than fresh water and that exposure to the acid at sublethal concentrations

TABLE 1. Literature survey of sublethal responses of salmonids to neutralized, composite whole kraft pulpmill effluent. Incipient sublethal thresholds for the various responses are summarized, or if not determined, the test concentration yielding the reported response is given. LC50 is synonymous with TL_m96 (Sprague 1969).

Species	Function or system affected	Nature of response	Fish size	Test temp. (C)	Concn tested	Sublethal threshold concn	Comments	Reference
Salmo gairdneri	Respiration	Elevated "cough" frequency	20.3–25.4 cm	11±1	—	0.08 96-h LC50	Response reduced after 2 h	Walden et al. 1970
" "	Circulation	Reduced arterial O_2 saturation	150 g	10	0.33–96-h LC50	—	No adaptation after 24 h	Davis 1973
Oncorhynchus nerka	Respiration	Elevated "cough" frequency	207–321 g	10.5±0.5	—	0.1–0.2 96 h LC50	Response reduced overnight	" "
" "	"	Ventilation vol up	" " "	" "	—	0.2 96 h LC50	" " "	" "
" "	"	O_2 uptake increased	" " "	" "	—	0.33 96-h LC50	" " "	" "
" "	Growth	Growth rate and food conversion efficiency decreased	2.4–2.8 g	15	—	0.08 96-h LC50	After 8 wk exposure	Webb and Brett 1972
" "	Behavior	Fish avoid effluent	3 cm	10	—	0.2 96-h LC50	Within 1 h exposure	G. M. Kruzynski (personal communication)
O. kisutch	Circulatory	Leukocyte count thrombocyte count reduced	juvenile	11±1	—	0.1 TL_m96	After 21 days exposure	McLeay 1973
" "	"	Blood neutrophil count elevated	"	11	—	0.25 TL_m96	After 200 days exposure	McLeay and Brown 1974
" "	Metabolism	Liver glycogen depressed	9.0±0.4 g	11	0.8 LC50	—	1/5 of initial level after 72 h exposure	McLeay and Brown 1975
" "	"	Plasma Glucose elevated	" " "	11	" "	—	3-fold increase after 96 h exposure	" " "
" "	"	Elevated plasma glucose and lactate, decreased liver and muscle glycogen	" " "	11	0.7 LC50	—	Following exercise and post-exercise recovery in effluent	" " "
" "	"	Plasma glucose elevated	juveniles	11	—	0.10 TL_m96	After 200 days exposure	Howard et al. 1972
" "	"	Blood and muscle lactate elevated	"	11±1	—	0.25 TL_m96	After 200 days exposure	" " "
" "	"	Muscle glycogen depressed	"	"	—	0.10 TL_m96	" " " "	" " "
" "	Energetics	Swimming ability impaired	"	13±0.5	—	0.20 TL_m96	Exercise in test chamber	Howard 1973
" "	Temperature tolerance	Reduced upper lethal temp	"	10	—	0.062–0.23 TL_m96	Lethal temp bioassay	" "
" "	Respiratory	Elevated cough frequency	post smolts	10	—	0.148 TL_m96	Evidence of adaptation	" "
" "	Growth	Growth rate enhanced	4–10 g	10–13	—	0.1–0.2 96-h LC50	After several wk exposure	Mason and Davis 1976
" "	" "	" "	juveniles	12±1	—	0.25 96-h LC50	200 day exposure	McLeay and Brown 1974
" "	Behavior	Feeding less vigorous	4–10 g	10–13	—	0.1–0.2 96-h LC50	Response lasted 2 wk then disappeared	Mason and Davis 1976
" "	"	Fish slow, "unresponsive"	"	12–13	—	0.15 96-h LC50	After several wk exposure	" " "
S. salar	Behavior	Fish avoid effluent	7.7–14.8 cm	17±0.2	—	Approx. .006 96-h LC50	"Vague" response	Sprague and Drury 1969

TABLE 2. Sublethal responses of salmonids to neutralized kraft bleach plant waste and waste from the production of unbleached pulp. The incipient sublethal threshold values are given. Data for *Oncorhynchus tschawytscha* refer to unbleached pulp effluent studies.

Species	Function or system affected	Nature of response	Fish size	Test temp (C)	Sublethal threshold concn	Comments	Reference
Oncorhynchus tschawytscha	Growth	Growth rate decreased	under-yearlings	7–13	0.14–0.35 TL_m96		Ellis 1967
"	"	"	juveniles	—	0.1–0.3 TL_m96	13–16 days exposure	Tokar and Owens 1968
			Neutralized Kraft Mill Bleach Plant Waste				
O. nerka	Growth	Growth rate decreased	alevins	8	0.05–0.1 96-h LC50	Egg to alevin development slowed	Servizi et al. 1966
"	Behavior	"Alarm response" diminished	fingerlings	8	0.4 96-h LC50	During acute toxicity bioassay	" " "
"	"	Orientation to water current affected	"	8	0.8 96-h LC50	"	" " "
O. gorbuscha	Growth	Growth rate decreased	alevins	8	0.05–0.1 96-h LC50	Egg to alevin development slowed	" " "

apparently interfered with the ability of saltwater-acclimated sockeye salmon to adapt to fresh water. Dehydroabietic acid produced bloating of the gut and accumulation of water in muscle tissue of freshwater sockeye, and loss of water from muscle in saltwater-adapted chum (*O. keta*), suggesting osmotic imbalance and differing modes of action, depending on salinity. Such responses could, of course, be the result of a general debilitation of some other physiological system due to resin acid toxicity with osmotic imbalance constituting one part of a generalized stress response. Such work with isolated individual toxicants may one day lead to identification of the major toxic fractions in KME which hopefully, can be removed from the waste prior to discharge. Such work will help in the technology required to develop a new era of "low toxicity" pulpmills.

Discussion and Recommendations

The foregoing analysis illustrates that a considerable body of knowledge has been amassed on sublethal effects of KME on salmon. Despite this information, regulations used by both Federal and Provincial agencies currently are partially based on acute toxicity bioassays. Such bio-

assays only tell whether or not effluent kills fish in a given time period and tell nothing of the more subtle, yet potentially equally hazardous sublethal effects. Based upon the current analysis for neutralized whole kraft mill effluent, some sublethal effects would occur in salmonids if regulatory agencies called for a dilution factor assuring 0.1 of the 96-h LC50 at the point of discharge. Most sublethal effects would be absent if 0.05 96-h LC50 was adopted as a dilution criterion. However, if on-site testing showed a sensitive response (i.e. some avoidance at 0.006 LC50 — Sprague and Drury 1969) was present, more stringent control might be required. This would also be the case if complications arose due to synergistic toxic effects caused by discharge of several toxic industrial wastes or the presence of low oxygen (see Sprague 1969, for discussion of synergistic toxic effects). To allow a good margin of safety for sensitive sublethal responses and provide a "buffer" against periodic toxic black liquor spills (Gordon and Servizi 1974), adoption of a dilution criterion of 0.02 LC50 would be highly desirable. Such dilutions may not prove practical for many mills unless in-plant water usage is vastly increased and diffuser pipes (Waldichuk 1974) are installed in well-flushed receiving waters. Caution, however, should be exercised in the installation of diffusers in stratified inlet situations, as waste with a high BOD may accumulate in deep, poorly circulated water, with little net transport away from the area (Tully 1949; Waldichuk 1974). These recommendations are based on current information, bearing in mind the difficulty of comparing results with effluent tested from a variety of mills by various procedures. Thus, the recommendations should be considered tentative and subject to revision with new knowledge.

A problem has recently come to light which involves the tainting of fish flesh caused by exposure to kraft mill effluent. Various salmonids and eulachons (*Thaleichthys pacificus*) have become tainted in British Columbia waters, rendering them unpalatable and of little value as commercial, recreational, or native Indian food fish. At present, the concentration required, length of exposure time, and the chemical nature of the compound(s) causing tainting are unknown. Some preliminary information indicates salmon and eulachons may become tainted in low concentrations of KME, possibly at dilutions below 0.02 of the LC50 advocated above. For this reason, caution should be exercised in applying the above criteria.

Currently, Federal and Provincial regulations deal with discharged waste toxicity in terms of responses of fish in acute toxicity tests. By expressing sublethal responses as some fraction of the acute LC50 test response, the simple acute toxicity bioassay becomes a useful tool for estimating desirable dilution factors to minimize sublethal effects. Thus, it is not necessary that the elaborate experimental apparatus often required for sublethal effect work always be applied to routine testing procedures. Sublethal effect tests can in many instances be confined to the laboratory, unless simple field tests can be developed, possibly involving simple hematology, cough frequency, or avoidance behavior tests. If standard acute toxicity tests are used as the basis of sublethal dilution criteria, these acute tests should involve rigorous bioassay procedures (Sprague 1969; Davis and Mason 1973) and be standardized by the use of reference toxicants (Davis and Hoos 1975).

A considerable effort must be made in research to accurately regulate pulpmill effluent discharge, identify its environmental effects, and minimize damage to aquatic communities. We know little of the life history of salmonids with regard to the effects of KME on downstream and returning migrants. Many coastal pulpmills are located in estuarine areas which serve as rearing areas for many species and points of salinity adaptation for anadromous salmonids. Virtually nothing is known of the effects of KME on aquatic food chains, and extensive studies of phytoplankton, zooplankton, and benthos are required. There is also a need to develop survey and monitoring techniques, as well as lethal and sublethal bioassay procedures, so that each region receiving KME wastes can be properly assessed with consideration of its own special chemical, physical, and biological characteristics. Attempts to apply criteria to individual situations without consideration of the local characteristics are bound to be unrealistic. Ideally, the kraft mill industry and aquatic resources must be made to coexist, providing that best available treatment technology is practiced and some compromise is made in environmental quality without serious impairment of important aquatic resources.

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Effects of Sublethal Concentrations of Pollutants on the Behavior of Fish[1]

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KLEEREKOPER, H. 1976. Effects of sublethal concentrations of pollutants on the behavior of fish. J. Fish. Res. Board Can. 33: 2036–2039.

Due to dilution and dispersion of pollutants in the natural environment, chronic exposure to subacute concentrations of such substances is likely to affect a much larger number of species and individuals than exposure to acutely morbid or lethal concentrations. Evidence points to the behavioral toxicity of subacute concentrations of pesticides affecting general locomotor behavior and orientated responses to environmental variables in particular. Complex interaction of these variables also may occur and the response to such interaction by fish may be affected by chronic exposure to organophosphate. Response modifications are often subtle and may require long-term monitoring.

KLEEREKOPER, H. 1976. Effects of sublethal concentrations of pollutants on the behavior of fish. J. Fish. Res. Board Can. 33: 2036–2039.

A cause de la dilution et de la dispersion des polluants dans le milieu naturel, l'exposition chronique à des concentrations subaiguës de telles substances affectera probablement un nombre beaucoup plus grand d'espèces et d'individus qu'une exposition à ces concentrations morbides ou létales aiguës. On a des preuves que des concentrations subaiguës de pesticides sont toxiques et affectent le comportement locomoteur en général et les réponses d'orientation à des variables du milieu en particulier. Il peut également se produire une interaction complexe des variables, et une exposition chronique aux organophosphates peut affecter la réponse des poissons à une telle interaction. Les modifications de réponse sont souvent subtiles et peuvent exiger un contrôle continu à long terme.

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CONCERN for the impact of massive chemical pollution on the biological quality of the aquatic environment has greatly stimulated research on the biological effects of potentially dangerous substances, commonly discharged as waste from industrial complexes or agricultural activities into watersheds and the oceans. Since the early 1960s when general public awareness and concern for the biological environment led to increased funding of research related to pollution, a vast amount of information has been accumulated on acutely morbid and lethal effects of pollutants on aquatic organisms, with particular emphasis on the relationships between these effects and the concentration of and the exposure time to the pollutants in question.

This approach, preponderant in the literature, seems to imply that acute mortality of aquatic organisms is considered to be the most important and urgent problem resulting from pollution. Although such mortality does take place and may have a dramatic impact on the general public when it affects a large number of organisms, its occurrence probably represents only a minor fraction of the total biological damage inflicted by a pollutant. The main argument in defense of this thesis is that, in general, acutely lethal or even morbid levels of a pollutant are most likely restricted to the vicinity of the locale of its release into the body of water in question. Beyond that region, depending on various physical and chemical factors, more or less rapid dilution and dispersion of the offending substance(s) occur. Effect of this common process is that only a relatively small mass of water, close to the polluting source, contains the highest concentrations of the pollutant which, from there, spreads into the contiguous masses of water. Dispersion, whose gradient will depend on many variables, leads to the presence of the diluted pollutant in a vastly greater mass of water likely to harbor a variety of ecologically significant conditions, species, and numbers of organisms. Therefore, I assume that, in general, a much greater biomass is exposed chronically to low, subacute concentrations of given pollutants than that confronted by acutely morbid or lethal levels of these substances. Biological effects of such chronic exposure to vari-

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ous pollutants have only recently become topics of enquiry. Research in this area has dealt with physiological, developmental, and behavioral aspects. The latter have received the least attention; they are the most difficult to assess quantitatively, particularly because of their variability, both among subjects and over time, and difficulties in the acquisition of reliable data. The resulting, almost total ignorance regarding the behavioral toxicology in fish of the most common pollutants at subacute concentrations should be of great concern to students of the environment. Behavior, be it based on genetic or acquired information or both, is a highly adaptive response to environmental variables of physical, chemical, or biological nature. Toxicological modification of any aspect of a behavioral pattern is not likely to be overt in its manifestation but may, and probably will, have subtle effects on the animal's capabilities to deal with the challenges of its environment. The very subtleness of such behavioral modification in the course of time creates additional difficulties for their identification, quantification, and the establishment of causal relationships between them and various polluting agents.

Among the many behavioral patterns in fish, locomotion and orientation behavior are of particular significance. They are instrumental in the procurement of food, mates, and nesting sites, and enable the animal to move adaptively and in a nonrandom fashion, in relation to physical, chemical, and biological conditions in the environment. Sensory information on the latter is acquired, processed, and integrated in the nervous system and fed into control mechanisms which based on genetically and, possibly, ontogenetically acquired information, determine the nature of the orientated locomotion required by the prevailing environmental system.

A complex biological system of this kind should be highly susceptible to stress by toxic agents in general, particularly in view of evidence that swimming performance can be affected by exposure to subacute concentrations of pollutants (Sprague 1971; Bull and McInerney 1974). Substances that affect basic neural function would be of special interest in this context; therefore, locomotion, especially orientation behavior, might present a suitable model for testing toxicological effects of pollutants on behavior in fish. Experimental rationale for such testing already existed and was derived from the main research activity in my laboratory: the analysis of general locomotor behavior and orientated locomotion. Over the past 20 yr, this endeavor has resulted in our ability to describe, quantify, and analyze, with a considerable degree of accuracy and reliability, the locomotor behavior of fish under controlled experimental conditions and, more recently, allowed my colleague and collaborator, Dr J. H. Matis, of the Institute of Statistics of this University, to develop mathematical models describing that behavior (Matis et al. 1974a, b, c, 1975). These developments provided us with a new and powerful tool to verify whether a particular environmental variable, natural or man-made, affects "normal" locomotor behavior and, if so, what the effects are. Precise, quantitative assessment of locomotion, be it "normal" or modified by experimental variables, requires monitoring of locomotor patterns over extended periods, resolution of these patterns into their basic components, and definition of these as to their magnitude, frequency, distribution, and interdependence over time. The basic components, which in their conjunction make up the locomotor pattern, are: turns, length and orientation of the steps between turns, and velocities. In our laboratory, these variables are determined electronically in the course of the monitoring process whose basic principles have been described previously in various papers (Kleerekoper 1969, 1976; Kleerekoper et al. 1970) and, therefore, will only be outlined briefly here.

Movements of a single fish, in a tank measuring 5.0 × 5.0 × 0.6 m, are monitored by a square matrix of 1936 photoconductive cells, on 10-cm centers, embedded in the floor of the tank, photosensitive faces upward. Collimated light is projected uniformly from overhead onto the surface of the water and projects a sharply contoured silhouette of the fish onto the photocell matrix, which is connected by an electronic interface with a small on-line computer. Electronic scanning of the x- and y-axes of the matrix determines the coordinates of a photocell whose electrical resistance has increased as a result of shading by the fish. This information, together with the real time of the shading event, is recorded on magnetic tape and stored on a memory pack. From these data, the above-mentioned components or variables of the locomotor pattern are computed and their behavior is analyzed as functions of time and space in the tank.

Because a number of accessory facilities, including the establishment of almost perfect laminar flow, permit the experimental creation of a variety of physical, chemical, or biological conditions, singly or in combinations, in all or part of the monitor tank, the locomotor behavior of the fish in response to such environmental variables can be analyzed and quantified.

A second system, represented by three monitor tanks, operates on the principle of multiple choice in which the fish has equal access to 16 radially oriented compartments guarded by photoelectric

gates in a cylindrical tank. As the fish moves about, entries, exits, and time of these events are recorded for subsequent analysis of the animal's orientation or "preference" or "avoidance" behavior. Physical and chemical conditions, singly or in combination, can be controlled and varied in any number of compartments.

The two monitor systems have been applied to pollution-related problems as well as to fundamental problems regarding locomotor control mechanisms in fish. They have allowed us to verify, over extended periods, the effects of previous exposure of the fish to subacute concentrations of pesticides on its "normal" locomotor behavior pattern and on its responses to naturally occurring environmental variables and their interactions. Conversely, the locomotor response of normal fish to pollutants could be studied.

Stochastic analysis of the many data, representing long periods and many fish, led Dr J. H. Matis to construct sensitive forecasting models of the locomotor behavior under control conditions, allowing the almost immediate detection of responses to environmental change too subtle for observation by more conventional techniques (Matis et al. 1974b). Among the results obtained so far with the approaches outlined above, with reference to pollution-related problems, I should like to emphasize those that demonstrate the existence of powerful interactions between physically and chemically independent variables which, when presented separately to the animal, elicit totally different responses than when in combination. Such interactions, to be differentiated from simple synergisms, have been demonstrated for copper ions and their gradients (Kleerekoper et al. 1972; Timms et al. 1972; Westlake et al. 1974); copper ions and temperature (Kleerekoper et al. 1973), and food odor and rates of water flow (Kleerekoper 1974; Rand et al. 1975). Goldfish (*Carassius auratus*) that had been exposed to parathion at a concentration of 0.33 ppm during 24 h exhibited a significant change in the orientation of their locomotion.

By the multiple choice, cylindrical monitor, Rand (1976) compared the locomotor behavior of goldfish before and after exposure to the organophosphate parathion at a concentration of 0.33 ppm during 24 h. Exposure at this subacute concentration resulted in a significant change in the orientation of locomotion in all nine fish tested. Moreover, this species, as well as largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*), exhibited decreased activity following exposure, accompanied by a highly increased sensitivity to external stimuli. Similar observations have been reported by Benke and Murphy (1974), Maki et al. (1973), Peterson (1974), and Matton and Laham (1969). The exposure to parathion significantly affected not only simple rheotactic response in the goldfish but, more interestingly, its response to interacting flow rates in a multiple choice situation. Evidence presented by Rand points to equally complex effects of parathion exposure in bass and bluegills.

Unexposed goldfish were attracted by food odor in slowly flowing water but avoided the odor/flow combination following parathion exposure. However, when confronted with four different rates of flow simultaneously, in combination with food odor, the responses changed significantly. Rand determined the occurrence of various statistical interactions of second order between rates of flow, odor and flow, and parathion.

All these results clearly point to the need to study behavioral responses, not in reaction to a single variable but to naturally occurring combinations of variables which, surely, prevail in the biological environment. Furthermore, our long-term recordings of general as well as orientated locomotion consistently demonstrate that due to inherent variability, short-term observations of locomotor behavior, as a rule, render quantitatively unreliable data.

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Monitoring Procedures for Chemical Carcinogens in Coastal Waters[1]

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DUNN, B. P., AND H. F. STICH. 1976. Monitoring procedures for chemical carcinogens in coastal waters. J. Fish. Res. Board Can. 33: 2040–2046.

Sampling procedures and analytical techniques have been developed for evaluating the contamination of coastal waters by polycyclic aromatic hydrocarbon carcinogens. The procedures involve extraction and purification of hydrocarbon fractions from marine sediments or organisms, and determination of compounds by thin-layer chromatography and fluorimetry, or gas chromatography.

Sediment samples in the vicinity of a sewage outfall showed elevated levels of benzo[*a*]pyrene (B[*a*]P). Mussels (*Mytilus edulis*) taken from the outer Vancouver harbor showed lower B[*a*]P levels in the summer than in the winter, perhaps a result of seasonal discharges of sewage and storm drain water into the harbor. Elevated levels of B[*a*]P in mussels growing near creosoted timbers or pilings suggested that creosote may be a significant source of B[*a*]P in the marine environment. Direct evidence for this suggestion was obtained by comparison of gas chromatographic profiles of polycyclic aromatic hydrocarbons isolated from mussels and from creosoted wood.

The procedures developed are rapid, sensitive, and reproducible. They appear to be suitable for application in large-scale monitoring systems for carcinogenic hydrocarbons in coastal waters.

DUNN, B. P., AND H. F. STICH. 1976. Monitoring procedures for chemical carcinogens in coastal waters. J. Fish. Res. Board Can. 33: 2040–2046.

Nous avons développé des protocoles d'échantillonnage et des méthodes analytiques permettant d'évaluer la contamination des eaux côtières par des hydrocarbures aromatiques polycycliques cancérigènes. Les protocoles comprennent l'extraction et la purification de fractions d'hydrocarbures de sédiments ou d'organismes marins et la détermination des composés par chromatographie sur couche mince ou par chromatographie en phase gazeuse.

Des échantillons de sédiments dans le voisinage d'un émissaire d'égout indiquent des niveaux élevés de benzo[*a*]pyrène (B[*a*]P). Des moules (*Mytilus edulis*) provenant du port extérieur de Vancouver ont des niveaux plus bas de (B[*a*]P) en été qu'en hiver, peut-être par suite de déversements saisonniers d'égouts et d'eaux pluviales dans le port. Les niveaux élevés de (B[*a*]P) observés dans des moules croissant à proximité de charpentes ou de piliers créosotés donnent à croire que la créosote peut être une source importante de (B[*a*]P) dans l'environnement marin. Nous en avons eu la preuve en comparant les profils chromatographiques gazeux des hydrocarbures aromatiques polycycliques isolés des moules avec ceux du bois créosoté.

Ces protocoles sont rapides, sensibles et reproductibles. Ils semblent convenir à des systèmes à grande échelle de contrôle continu d'hydrocarbures cancérigènes dans les eaux côtières.

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A proper appraisal of the contamination of the marine environment must consider not only pollutants with acute toxicity, but also those which have delayed, sublethal effects. Some of the potentially most dangerous, although as yet little studied, marine pollutants are the chemical carcinogens. Because of possible economic damage to fisheries and aquaculture, and potential danger to man from consuming carcinogen-contaminated seafoods and marine products, the importance of investigating the distribution of carcinogenic compounds in the oceans cannot be overemphasized.

In recent years emphasis has been placed on the development of monitoring systems capable of giving advance warning of the contamination of the environment. Such monitoring systems must rely either on chemical procedures for the detection of contaminants, or on the response of sensitive biological indicators. Data presented in

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this paper illustrate a chemical approach to the monitoring of the marine environment for carcinogenic compounds. Other approaches, notably those using tumors in fish (Stich and Acton 1975; Stich et al. 1976a, b) or growth abnormalities in lower organisms (Ishio et al. 1971), are also feasible. Ultimately, the combined application of chemical and biological assays should provide the most sensitive and reliable warning system for carcinogen contamination.

The investigations reported here deal with the class of chemical carcinogens known as the polycyclic aromatic hydrocarbons (PAH), and in particular with potent carcinogen benzo[*a*]pyrene (B[*a*]P). Polycyclic aromatic hydrocarbons are reported to be present in bottom sediments (Blumer and Youngblood 1975) and marine organisms (ZoBell 1971). However, there have been no systematic surveys to determine the sources, geographical distribution, or fate of these compounds in the oceans.

Materials and Methods

The procedures used for the extraction and purification of PAH from marine samples will be more fully described elsewhere (Dunn 1976) and only an outline of the techniques will be given here. The methods are adapted from those developed by Howard et al. (1966) for the measurement of polycyclic aromatic hydrocarbons in foodstuffs. The original procedures have been modified in the interest of speed, simplicity, reliability, and economy of reagents.

Figure 1 shows a flowchart of the procedures. The left portion of the chart shows the basic procedure for the isolation of PAH and the fluorimetric determination of B[*a*]P. Samples (20–60-g tissue or 10–40-g sediments) plus a known amount of radioactive B[*a*]P are extracted by alkaline digestion, and the hydrocarbons then partitioned into iso-octane. Column chromatography on Florisil removes pigments, and separates the hydrocarbons into an iso-octane eluate, which is normally discarded, and a benzene eluate, which contains PAH plus interfering materials. After concentrating the latter fraction into iso-octane, the PAH are selectively extracted using dimethylsulfoxide (DMSO). The PAH are then recovered from the nonvolatile DMSO by addition of water and back-extraction into fresh iso-octane. Thin-layer chromatography is used to isolate B[*a*]P from the purified PAH fraction, and the compound is measured fluorimetrically. Measurement of the amount of radioactivity in the final fluorimetry sample permits the calculation of the percentage recovery of the compound through the procedures. All values reported in this paper are corrected for losses, which generally ranged from 20 to 40%. The fluorimetric determination of B[*a*]P has a sensitivity of approximately 0.1 μg/kg for a 25-g sample and a precision of better than 10% (Dunn 1976).

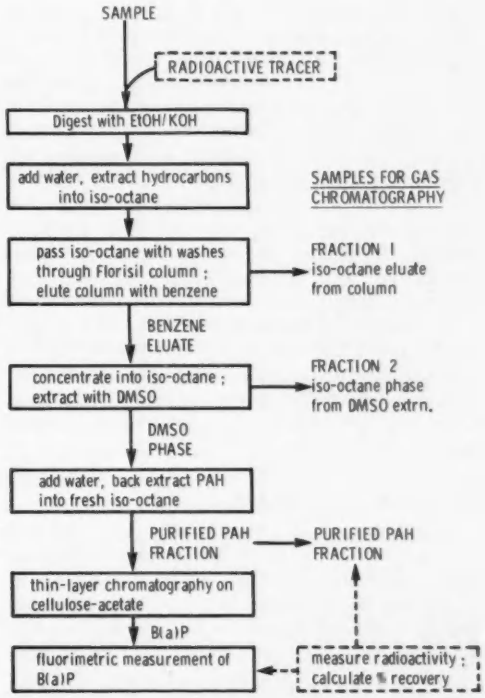
SAMPLE
RADIOACTIVE TRACER
Digest with EtOH/KOH
add water, extract hydrocarbons into iso-octane
SAMPLES FOR GAS CHROMATOGRAPHY
pass iso-octane with washes through Florisil column ; elute column with benzene
FRACTION 1 iso-octane eluate from column
BENZENE ELUATE
concentrate into iso-octane ; extract with DMSO
FRACTION 2 iso-octane phase from DMSO extrn.
DMSO PHASE
add water, back extract PAH into fresh iso-octane
PURIFIED PAH FRACTION
PURIFIED PAH FRACTION
thin-layer chromatography on cellulose-acetate
B(a)P
fluorimetric measurement of B(a)P
measure radioactivity ; calculate % recovery

FIG. 1. Flowchart of hydrocarbon extraction and purification procedures.

The iso-octane eluate from the Florisil column and the iso-octane phase from the DMSO extraction are normally discarded when samples are processed for the fluorimetric determination of B[*a*]P. These fractions, which are designated as Fractions 1 and 2 in Fig. 1, may be saved and analyzed for paraffinic and other hydrocarbons by gas chromatography. In addition, a portion of the purified PAH fraction may be diverted from thin-layer chromatography and analyzed by gas chromatography.

Results

Benzo[*a*]pyrene in Bottom Sediments

To investigate effluent from sewage treatment plants as a possible source of B[*a*]P contamination in coastal areas near cities, samples of bottom sediments were taken in the vicinity of the outfall of the Iona Island sewage treatment plant, south of Vancouver. This plant, situated to the south of the mouth of the north arm of the Fraser river, gives primary treatment to mixed sewage and storm drain wastewater. It has a design capacity of 320,000 kl/day. The effluent is discharged onto an intertidal mud flat immediately to the south of a jetty. Core samples of sediments were

taken to a depth of 5 cm at low tide, and the material from each core was thoroughly mixed. A representative portion was dried at 80 C for the determination of moisture content, and then heated at 550 C for 24 h for the determination of the crude organic content by weight loss on ignition. An undried sample of sediment was processed for the determination of B[*a*]P content, and the concentration of carcinogen expressed as micrograms per kilogram total dry sediment weight, or micrograms per kilogram sediment organic content. The data (Fig. 2) indicate that expressed either way, there is a gradation of contamination towards the outfall. This is particularly evident with the results expressed in terms of sediment weight, where the two samples closest to the outfall have a contamination greater than 3 times that of the next most polluted sample.

Benzo[*a*]pyrene in Mussels

The measurement of B[*a*]P in mussels (*Mytilus edulis*) may be an excellent procedure for determining the degree of contamination of bodies of water by polycyclic aromatic hydrocarbons (Dunn and Stich 1975). In anticipation of the use of this technique in large-scale monitoring systems for carcinogenic hydrocarbons, sampling procedures for mussels were evaluated. No significant difference in B[*a*]P levels was noted between mussels from the same location but taken at different depths in the intertidal zone. Similarly, analysis of mussels of different sizes (35–60 mm) taken at the same time and from the same location showed no significant differences in B[*a*]P content. However, the B[*a*]P content of mussels was found to vary in samples collected at the same location but at different times of the year.

Mussels were collected from five stations on the south shore of the outer Vancouver harbor (Fig. 3). These stations differed in the proximity and type of potential pollution sources. Station 1, Spanish Banks, is a recreational beach at least 2 km from the nearest wharf. Station 2 is on the beach facing the Royal Vancouver Yacht Club wharf. Mussels in this location may be subject to contamination from creosoted pilings as well as from auxiliary engines on the sailing craft moored in this area. Station 3 is on rocks at Kitsilano Point, a recreational beach. Station 4 is on a concrete bridge abutment at the north end of the Burrard bridge, spanning False Creek. Mussels in this area are encircled at a distance of 3–5 m with a barricade of creosoted timbers which protects the bridge abutment from shipping. Station 5 is on concrete at the eastern end of False Creek, a poorly flushed tidal inlet with many wharfs and surrounded by light industry.

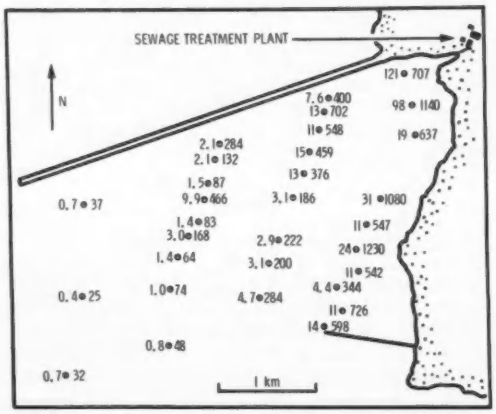

FIG. 2. Concentrations of B[*a*]P in sediments in the vicinity of the Iona Island sewage treatment plant. Values to the left of (○) are micrograms B[*a*]P per kilogram dry sediment, while those to the right are micrograms B[*a*]P per kilogram sediment organic content.

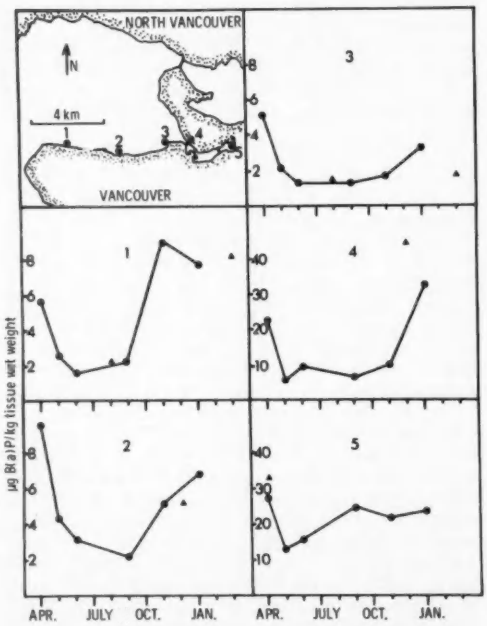

FIG. 3. Seasonal variations in the concentration of B[*a*]P in mussels (*Mytilus edulis*) from five Vancouver locations. ▲ January 1974 to March 1975; ●—● April 1975 to January 1976.

All stations are subject to possible contamination by sewage and storm drain effluent. Vancouver has a combined storm drain and sewer system. During periods of heavy rainfall the amount of combined effluent is greater than the capacity of the Iona Island sewage treatment plant, and a proportion of it is discharged directly without treatment into the outer Vancouver harbor through a number of submarine outfalls.

Levels of B[*a*]P in samples taken from the five locations between April 1975 and January 1976 are presented in Fig. 3, along with scattered data obtained from earlier samples (1974 and early 1975). Levels of B[*a*]P were highest at the two stations in False Creek, and lowest at Kitsilano Point. At all five stations there was a tendency towards lower levels of B[*a*]P in the summer months. This tendency was most pronounced at stations 1 and 2, where levels in the winter were as much as 5 times the levels in mid-summer. The degree and exact pattern of the fluctuations depended considerably on the site. Thus between September and November 1975, there was a sharp increase in the B[*a*]P content of mussels at stations 1 and 2, while there was only a slight rise at stations 3 and 4 and a drop at station 5.

Geographic Variation in Benzo[*a*]pyrene Levels in Mussels

The excellent geographical resolution possible when using attached organisms as bioaccumulators for toxic chemicals is shown by an investigation conducted in the vicinity of a wharf in the Vancouver area. The wharf, measuring approximately 25 × 100 m, is constructed of concrete and supported on concrete pillars. A floating dock attached to the wharf serves as a mooring for several small vessels. At intervals around the wharf, creosoted pilings and untreated floating logs serve as a bumper system, and at the eastern end of the wharf there is a substantial barricade of creosoted timbers. Aside from the single wharf, the area consists of a relatively isolated rocky beach with no permanent shoreline structures. Mussels were collected from the immediate vicinity of the wharf and along the shore to either side. Figure 4 indicates that the wharf and its associated structures represent a point source of B[*a*]P contamination. Levels were highest in mussels in the immediate vicinity of the wharf and dropped off at locations removed from the wharf area. Mussels taken from rocks underneath and near the wharf were contaminated to the extent of 54–78 μg/kg wet tissue wt, while those growing directly on the creosoted barricade were contaminated with 215 μg/kg, and those on rocks 1 m from the barricade with 172 μg/kg. The

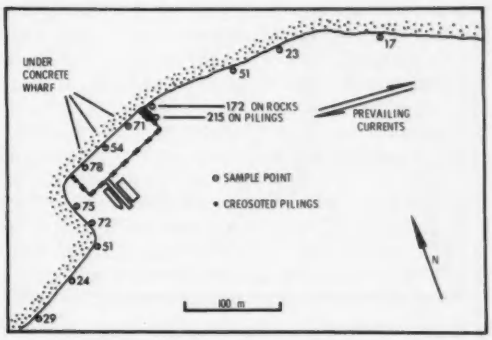

FIG. 4. Concentrations of B[*a*]P in mussels (*M. edulis*) in the vicinity of a wharf. Values are micrograms B[*a*]P per kilogram wet weight.

pattern of contamination suggests that the creosoted pilings and timbers rather than the moored vessels are the major source of contamination. The fact that levels of B[*a*]P in mussels in this area are much higher than those generally found near creosoted structures (for example stations 2 and 4 in Fig. 3) may reflect the age of the treated timber. The creosoted material at the wharf in Fig. 4 is relatively new, and retains a tarry residue on its surface, while the timber at the other locations is older and much weathered.

Gas Chromatographic Analysis

Besides providing a purified B[*a*]P sample for fluorimetry, the extraction and purification procedures developed can provide fractions for gas chromatographic analysis. Fraction 1 (Fig. 1) contains hydrocarbons which do not adhere to Florisil during elution with iso-octane. Fraction 2 contains material which is eluted from the column only with benzene, but is not subsequently extracted into DMSO. The chemical nature of Fractions 1 and 2 has not been investigated, but probably consists mainly of paraffinic hydrocarbons. If the sample size is adequate, a portion of the purified PAH fraction may be diverted for gas chromatography. Figure 5 presents gas chromatographic profiles of Fractions 1 and 2 and the purified PAH fraction isolated from mussels collected in August 1975 from station 4 (Fig. 3). The purified PAH fraction extracted from a small (5 mg) sample of creosoted wood from the pilings in this area is shown for comparison purposes.

Chromatograms of Fractions 1 and 2 show the feasibility of using the sample processing scheme described not only for aromatic hydrocarbons, but also for the simultaneous preparation of

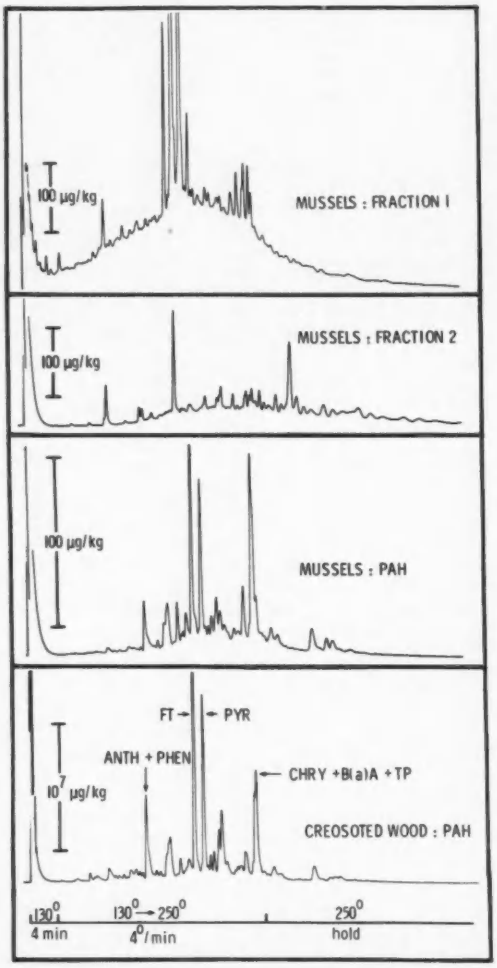

FIG. 5. Gas chromatography of hydrocarbon fractions from mussels and from creosoted wood. Abbreviations: ANTH, anthracene; PHEN, phenanthrene; FT, fluoranthrene; PYR, pyrene; CHRY, chrysene; B[*a*]A, benz[*a*]anthracene; TP, triphenylene. Chromatography was carried out on dual columns, ⅛ in. × 10 ft packed with 2% OV-7 on Chromosorb W HP 80-100 mesh. Helium flow was set for an average linear gas velocity of 7 cm/s, and detection was by flame ionization. Approximate relationship between peak height and sample contamination for a midchromatogram peak is indicated for each trace.

fractions containing other hydrocarbons of interest. An investigation comparing the nature of the hydrocarbons in these two fractions with the paraffinic hydrocarbon fractions obtained using other procedures appears justified. The PAH fractions from both mussels and creosoted wood contain a number of peaks which may tentatively be identified on the basis of the retention time of standards. The identity of four of the major PAH peaks is indicated on the creosoted wood trace. Benzo[*a*]pyrene is one of the minor peaks to the right of the chromatograms, and is usually not readily identifiable. There is a remarkable similarity between the chromatographic profiles of the PAH fraction from mussels, and that from creosoted wood from the same area. All major peaks in the creosoted wood sample are represented in the tissue sample, with in most cases only minor differences in the relative amounts of the different compounds.

Discussion

Coastal waters are one of the most productive areas of the oceans, and they are also the ultimate disposal grounds for most of the waste products of our industrial civilization. To prevent any destruction of those zones that are suitable for fisheries or aquaculture, the degree and type of contamination in the marine environment must be assessed. Very little is known about the distribution of carcinogenic agents in the oceans and their accumulation in edible marine organisms. Considering the great economic and health implications, this lack of information is difficult to understand. Before embarking on large-scale aquaculture programs, a proper understanding of the pollution of estuaries, shorelines, and intertidal zones by chemical carcinogens appears a necessity.

We had several objectives when developing procedures for the measurement of chemical carcinogens of the polycyclic aromatic hydrocarbon class. The procedures must be simple, rapid, and economical so that large numbers of samples can be analyzed. They must be sensitive, so that baseline levels of pollution can be measured, and reproducible, so that analytical results can be compared within and between laboratories. Rather than immediately trying to develop procedures for the simultaneous determination of several agents, we have concentrated on the development of techniques for the determination of one single compound, the potent and well studied carcinogen benzo[*a*]pyrene. Our aim was to use the level of B[*a*]P as an indicator of the possible presence and amount of other related carcinogens. This is analogous to the use of a single species, *Escherichia coli*, as an indicator for the bacteriological contamination of water. Benzo[*a*]pyrene is present in a variety of petroleum products, in coal tar products, exhausts from internal combustion engines, and fallout from urban air pollution. All these sources contribute to the

contamination of productive coastal waters by carcinogenic compounds.

When using chemical techniques to detect pollutants in shallow waters, there are three potential types of samples, each with its own sampling characteristics. Water samples offer the advantage of being universally obtainable in any size desired, but have several disadvantages. Levels of poorly soluble compounds such as PAH are often extremely low. Geographical resolution is usually poor due to currents and tides, and transient discharges are difficult to detect as the samples offer no integrating effect. We have, therefore, concentrated on the analysis of the two other sample types. Sediment samples are obtainable in large sizes and often contain high concentrations of pollutants. The samples have a substantial integrating effect and offer good geographical resolution, especially when current patterns, sediment origins, and settling rates are known. Marine organisms often have high residue levels due to bioaccumulation processes, and because of their consumption by man are usually the samples of most interest. Geographical resolution is excellent when using sessile species, and the continuous uptake and discharge of pollutants allows organisms to act as integrators, responding to the time-average of pollution in a given area.

Data presented in this paper on the analysis of sediments from the vicinity of the Iona Island sewage treatment plant outfall (Fig. 2) shows the utility of bottom samples in investigating a point source of pollution. The gradient of B[*a*]P contamination towards the outfall strongly suggests that it is a major contributor to the burden of carcinogenic chemicals in the Fraser estuary.

We have previously shown that the level of B[*a*]P in mussels from remote areas is at or below the level of detectability (Dunn and Stich 1975). In contrast, appreciable amounts of B[*a*]P were found in mussels from urbanized areas. Levels of contamination are particularly high in the vicinity of wharfs and marinas, and the association of high tissue levels with proximity to creosoted pilings and timber suggests that treated wood may be a major source of PAH (Fig. 4 and Dunn and Stich 1975). This circumstantial evidence is strongly supported by the marked similarity between the gas chromatographic profiles of PAH isolated from mussels and from creosoted pilings (Fig. 5). Using different techniques, Zitko (1975) has also implicated creosote in the contamination of marine organisms.

Mussels from five stations in the outer Vancouver harbor all showed lower levels of B[*a*]P in the summer than in the winter. The degree and exact pattern of the seasonal fluctuations, however, varied considerably at the five stations, even though they are in the same body of water and quite close to one another. This suggests that the variations are more likely to be attributable to seasonal changes in pollution than to something intrinsic in the bioaccumulator system, such as variations in B[*a*]P uptake or retention with water temperature or breeding cycle. Interestingly, the fluctuations at station 2, the Royal Vancouver Yacht Club, are in the opposite direction to those which would be expected if auxiliary engines on boats were a major source of contamination. Use of outboard and inboard engines is at a maximum during the summer sailing season, while the levels of B[*a*]P in mussels are at a minimum during this time.

One plausible explanation for the origin of the variations in B[*a*]P content of mussels in the Vancouver area is that at least a proportion of the contamination at each station results from sewage and/or drainage from land. Overflow discharges from Vancouver's combined sewer and storm drain system occur infrequently in the summer, but are relatively common during the winter rainy season. Wastewater from roads will contain oily residues which have built up during dry spells. These residues are likely to contain appreciable quantities of B[*a*]P. Investigations in this laboratory have found up to 22,000 μg B[*a*]P/kg of used crankcase oil (B. P. Dunn unpublished data). Sewage treatment plants have been shown to reduce the concentrations of PAH in wastewater (Borneff and Kunte 1967). Because during rainstorms a large fraction of the oily residues on roads is flushed into the harbor without treatment, overflow discharges may contribute more B[*a*]P to Vancouver waters than the continuous discharges of the Iona Island plant. Further investigation of this question by directly examining the concentrations of B[*a*]P in the various effluents may be profitable.

Seasonal variations in the B[*a*]P content of mussels have little effect on the relative ranking of the five Vancouver outer harbor stations in terms of degree of pollution, provided that samples taken at one time are compared. However, it is evident that in any full-scale monitoring program, great care will have to be taken when comparing samples taken at different sites and at different times. It is also evident from the marked variations in B[*a*]P contamination seen in one body of water (Fig. 2, 3, and 4) that multiple samples are necessary to fully define the degree of contamination of an area.

Measurement of B[*a*]P in sediments and organisms offers a powerful tool in the determination of the contamination of coastal waters by carcinogenic compounds. It can be used for obtaining an overall picture of the distribution of

PAH and for the investigation of specific areas of interest. Detailed studies of an area can give circumstantial evidence pointing to sources of contamination. For direct demonstration of the identity of pollution sources, an approach based on the "fingerprinting" of PAH contamination using gas chromatography appears promising.

A final use for the measurement of B[*a*]P in tissues would be to evaluate procedures used for the cleaning of contaminated seafoods. When creosote contaminated mussels were moved to tanks with clean circulating water, they lost B[*a*]P exponentially, with a half-life of approximately 2 wk (Dunn and Stich 1976). This retention time is much greater than that of bacteria in mollusks, suggesting that current depuration procedures designed to remove bacterial contamination from seafoods such as oysters are inadequate for the removal of carcinogen contamination.

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Sublethal Effects of Environmental Stressors, Natural and Pollutional, on Marine Fish Eggs and Larvae[1,2]

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Sublethal effects of environmental changes on marine fish eggs and larvae are reviewed within a framework of concepts supplied by Bartholomew (1964), Sprague (1971), and Selye (1952). Such effects are those a) elicited through application of stress at one level of organization or development, b) recognized through the appearance of altered structure or function at a later stage of development, and c) whose significance is fully manifested as lower survival potential at a further stage of development. A number of sublethal effects are marshalled in terms of type of biological response and inferred consequences. Data suggest that a variety of stress–stressor systems may trigger a limited number of organismic responses, often appearing to involve the same physiological and biochemical mechanisms. Most sublethal effects appear to be biochemical in origin, elicited through physical or chemical change, and expressed in terms of histological, morphological, physiological, or ethological response. A need is expressed for an expanded and more unified enquiry into the origin, recognition, and significance of sublethal effects.

ROSENTHAL, H., AND D. F. ALDERDICE. 1976. Sublethal effects of environmental stressors, natural and pollutional, on marine fish eggs and larvae. J. Fish. Res. Board Can. 33: 2047–2065.

Nous passons en revue les effets sublétaux de changements dans l'environnement sur les œufs et les larves de poissons de mer, dans le cadre des concepts mis de l'avant par Bartholomew (1964), Sprague (1971) et Selye (1952). Ces effets sont: a) ceux qui sont provoqués par application d'un stress à un niveau d'organisation ou de développement, b) ceux qui sont perçus par l'apparition d'une structure ou d'une fonction modifiée à un stade ultérieur de développement et c) ceux dont la signification se manifeste entièrement sous forme d'une survie amoindrie à un stade ultérieur de développement. Un certain nombre d'effets sublétaux sont classés en termes de type de réponse biologique et de conséquences qui en sont déduites. Les données donnent à croire qu'une variété de systèmes stress–agents de stress peuvent déclencher un nombre limité de réponses organismiques, paraissant souvent impliquer les mêmes mécanismes physiologiques et biochimiques. La plupart des effets sublétaux semblent être d'origine biochimique, pouvant être déclenchés par un changement physique ou chimique, et être exprimés en termes de réponse histologique, morphologique, physiologique ou éthologique. Nous exprimons le besoin de recherches plus poussées et plus unifiées sur l'origine, la reconnaissance et la signification des effets sublétaux.

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MANY low levels of natural or man-made environmental changes are within the normal range of adaptation of living organisms and are tolerated indefinitely. Greater changes, although they may be resisted for a time, ultimately and directly result in death of the organism. Between these zones of tolerance and resistance lies a boundary region of sublethal responses, where the survival potential of the organism is reduced, indirectly at a later stage, as a consequence of the stress imposed by environmental circumstances. Sublethal effects are of concern because of their often subtle nature. They may often occur and go unrecog-

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nized at the individual level and proceed until their significance is interpreted at the population level, after the damage is done.

Sublethal effects may be defined as those responses to environmental change — histological, morphological, physiological, or ethological — that may be induced in one stage of development but be expressed in a later stage of organization or development in terms of reduced survival potential. Sprague (1971) considers the significance of sublethal effects in terms of levels of biological organization. For example, the functional biochemistry of a cell may determine the efficiency of a tissue or organ. In turn, tissue or organ efficiency will influence the performance of the individual organism. Finally, survival potential or success of groups of organisms in an ecosystem is related to performance of the individuals comprising the group. Bartholomew (1964) summarized the concept very succinctly. He concluded that "there are a number of levels of biological integration and . . . each level finds its explanation of mechanisms in the level below and its significance in the levels above" (Sprague 1971). Therefore, identification of small changes occurring in an organism is only one stage in comprehending sublethal effects. Just as pertinent is the often more complex task of identifying the consequences to the individual and the ecological significance of these often subtle responses in the population.

The accelerating pace at which man-made changes are occurring in the aquatic environment seems to have channeled much of recent enquiry into examination of current substantial environmental concerns, in the search for immediate and expedient solutions. Also, the technology underlying the search is largely expedient, being based largely on measurement or inferences arising from response to lethal circumstances. Hence, much of the pertinent literature refers to lethal effects that relate to natural or man-made environmental changes affecting survival directly. The importance of understanding sublethal responses has been well recognized, at least since the early 1960s (Tarzwell 1960, 1965). In the intervening years, attention has expanded from fresh water to include marine pollution (FAO 1971a, b). Yet relatively little synthesis of data appears to have occurred with regard to sublethal effects of pollutants, or to the indirect constraints placed on survival of marine organisms developing at limiting levels of natural environmental entities.

In this paper emphasis will be placed on identification of stress–stressor systems affecting marine fish eggs and larvae. We apply Bartholomew's (1964) and Sprague's (1971) concepts to levels of organization within the individual and to stages of ontogenetic development within the population. We shall discuss sublethal responses elicited in one stage, whose significance with respect to survival is expressed or likely to be found in ensuing stages of organization. Hence, we envisage a matrix of levels of organization. On one axis are found the units of organization — the cell, tissue, organ, individual, and group; on the other axis are the ontogenetic stages — the egg, embryo, larva, juvenile, adult, and gonadal tissue.

This paper is a limited review, in which a more comprehensive format is sought for better understanding of the general problem of sublethal effects. Accordingly, the authors have made liberal use of their own published and unpublished work, while referring to approximately one quarter of the pertinent literature at their disposal.

Sublethal Effects of Stress–Stressor Systems

In attempting to catalogue sublethal effects, the nature of the response to stress and its consequences are emphasized rather than the nature of the stressor. We are mindful of Selye's (1952) "general adaptation syndrome," whereby the organism appears to respond in a limited number of specific ways to a broad range of applied stressors. For example, low incubation temperature and some poisons (e.g. cadmium) have a common effect on hatching (Alderdice and Forrester 1971; H. Rosenthal and D. F. Alderdice unpublished data). In each case there is a diminished level of embryonic activity within the egg. Presumably, reduced embryonic movement results in an increased concentration of hatching enzyme in the head region, as the perivitelline fluid is not stirred by normal body movements. Capsule rupture occurs in the head region, the head emerges, the hatching process ceases, and the embryo eventually dies.

It is important to recognize that some combinations of levels of natural environmental factors may evoke sublethal responses, on which a response to pollutants may or may not be superimposed. Some responses may be increased by addition or potentiation. In Table 1 some sublethal effects are listed that may result from exposure to particular levels of natural and unnatural environmental factors. In many of these, the initial function affected, often inferred after the fact, is related to the first recognized consequences to influence subsequent survival. In many instances the sequence occurs in closely following ontogenetic stages. Of course, once the result of sublethal exposure is fixed by structural or functional modification in one stage, the result will affect later ontogenetic stages in varying degree, depending on the severity of the initial sublethal

response. We consider the natural environmental factors first. A few examples illustrate the findings of numerous investigators who have examined effects of temperature, salinity, dissolved oxygen, or their combined effects.

Natural Environmental Factors

As summarized by Blaxter (1969), there exists a close realtionship between temperature and incubation time. Although hatching is not a distinct ontogenetic stage, incubation time from fertilization to hatching, as well as hatching success, can be important to the survival potential of a species developing under different ecological circumstances.

Incubation temperature has a marked influence on larval size at hatching, and on the time course of yolk utilization. In Pacific herring (*Clupea harengus pallasi*) temperature and salinity influence larval size at hatching (Alderdice and Velsen 1971). Near-maximum larval size occurs on a "ridge" running from combinations of higher salinity and lower temperature to those of lower salinity and higher temperature (high/low–low/high interaction). In the same study, near-maximum hatches of viable larvae occurred on a low/low–high/high salinity–temperature ridge. Maximum hatch of viable larvae occurred near 8.3 C and, in a further investigation of osmoregulation (unpublished data), at incubation salinities of 12–18‰ (S). Data, similar in many aspects, were obtained for desert pupfish, *Cyprinodon macularius* (Kinne and Sweet 1965).

Kinne and Kinne (1962) concluded for eggs of *C. macularius* that retardation of development rate and narrowing of the range of salinity–temperature tolerance resulted from reduction of ambient dissolved oxygen concentrations available to the eggs at higher salinities and temperatures. Combined effects of salinity, temperature, and dissolved oxygen have been shown to influence viable hatch of Pacific cod (*Gadus macrocephalus*) eggs (Alderdice and Forrester 1971). Eggs of this species appear euryhaline, euryoxic, and stenothermal. Maximum and near-maximum hatches of viable larvae occurred at temperatures of 3–4.5 C, over a broad range of salinities (13–23‰ S), and at dissolved oxygen concentrations above 2–3 ppm. Braum (1973) found that larval size at hatching in Atlantic herring (*Clupea harengus harengus*) eggs was reduced considerably when dissolved oxygen levels were maintained below 50% of saturation through the incubation period.

Reduced larval size at hatching, associated with environmental conditions of incubation, is judged as being analogous to a sublethal response. Smaller larvae with smaller yolk sacs could occur through increased costs of maintenance metabolism during embryonic development, at the expense of metabolism contributing to growth. They could have a shorter period between hatching, initiation of feeding on exogenous foods, and successful learning of prey-capture manoeuvres. However, smaller larvae with larger yolk sacs often appear to hatch "prematurely" under stressful incubation conditions. Such larvae could spend a longer than normal period in the vulnerable yolk-sac stage. In both instances, smaller larvae at hatching would be exposed to predation for a further period of growth, the period required for them to achieve the initial size of larger larvae incubated under more favorable circumstances.

Anatomical and behavioral anomalies also occur among Pacific herring larvae from eggs incubated at limiting salinity–temperature combinations (Alderdice and Velsen 1971). At temperatures below 5 C, larvae hatched with missing or rudimentary lower jaws. One such group (7.83‰ S) subsequently failed to develop lower jaws and showed no feeding behavior. Another group at 25‰ S eventually developed lower jaws of normal appearance and showed typical prey-capture reactions; however, survival to yolk exhaustion in the group was very low. A third group, incubated at a near-optimal temperature but low salinity (9.0 C, 5.0‰) had normal lower jaws at hatching. Yet the larvae were very inactive and showed few prey-capture reactions. Obviously both salinity and temperature are involved in the normal sequence of anatomical and behavioral development. Therefore, circumstances interfering with feeding ability and prey-capture behavior of larvae may be initiated in the egg. The resulting disruption in the sequence of following events can lead to inadequate food-gathering capacity and unfavorable growth of the hatched larvae.

We have discussed briefly a few ways by which limiting levels of natural environmental circumstances can induce sublethal responses in fish eggs and larvae. Such responses may also occur when alteration of natural environmental factors is induced on a local scale by man's activities. Hydroelectric dams, power plants, and desalination plants may modify salinities and temperatures in estuaries and shallow coastal areas. Edsall and Yocom (1972) documented heavy kills of fish larvae entrained in the cooling water systems of various power plants. Powles (1974), working with eggs and larvae of the bay- and estuary-spawning Australian anchovy (*Engraulis australis*), stated that vast numbers of eggs must pass through cooling condensers. He found survival of late developmental stages of eggs from

TABLE 1. Summary of some observed responses to environmental alteration considered as sublethal effects. These are shown in relation to ontogenetic stages of development in which they are observed and to known or possible consequences at later stages of development. For example, response to stress imposed at fertilization may be observed first as tissue anomalies in advanced embryos, whose significance to survival is expressed later as altered behavior in hatched larvae.

Stage of organization where stress is imposed or recognized	Observed or deduced response to stress (altered structure or function)	Observed or suspected consequences of response to stress
Sex products		
Sperm (prior to fertilization)	Reduction in motility	Reduced fertility
	Reduced fertility	Reduced rate of fertilization
	Gene damage	Embryonic malformations
Eggs (unfertilized and during fertilization)	Changes in properties of egg membranes, related to	
	surface structure of capsule	reduced rates of gas diffusion, respiration
	water uptake during and after fertilization	changes in osmoregulatory capacity
		changes in buoyancy of pelagic eggs (changes in transport, distribution and location in water column)
	rate of fertilization	reproductive success
Embryonic development (early and advanced)	Biochemical effects	
	changes in ATP levels	energy deficit
		retarded development
		necrotic tissue
		dedifferentiation
		organ malformation
	changes in enzyme activity	Interference with general metabolism and biosynthetic processes
		retarded development
		reduced yolk/energy conversion
		smaller larval size at hatching
		reduced hatching success
	Physiological effects	
	respiration changes	changes in embryonic growth rates
		changes in incubation rate
	embryonic heart rate	retarded development
	Morphological effects	
	unusual shape of blastodisc	embryonic malformations (?)
	deformation of blastomeres	embryonic malformations (?)
	irregular cleavage of blastomeres	embryonic malformations (?)
	amorphous embryonic tissue (no definite embryo formed)	no viable hatch
	yolk deformation	impaired yolk utilization, respiration (?)
	yolk-sac blood circulation not well developed	impaired yolk utilization (?) respiration (?)
	organ malformations	
	bent body axis	impaired swimming, feeding, escape reactions
	elongated heart tube	impaired blood circulation (?)
	eye malformations (see also yolk sac larvae)	impaired vision, prey hunting, photoaxis
	malformed otoliths and/or otic capsules	impaired equilibrium, swimming, prey hunting
	Behavioral effects	
	embryonic activity reduced	reduced mixing of perivitelline fluid affecting respiration,

TABLE 1. (*Concluded*)

Stage of organization where stress is imposed or recognized	Observed or deduced response to stress (altered structure or function)	Observed or suspected consequences of response to stress
		distribution of hatching enzyme; retarded development, abnormal hatching process
	pectoral fin movements reduced	as above (embryonic activity)
Larvae at hatching	Altered hatching parameters	
	change in duration of hatching period	altered distribution, density of larvae in time and space
	increased or decreased incubation time	desynchronizing of food availability at time of first feeding
	reduced viable hatch	reduced survival potential at population level
	smaller larval size at hatching	reduced biomass, increased susceptibility to predation
Yolk-sac larvae	Buoyancy anomalies	difficulty in maintaining position in water column
	Swimming behavior	
	inability to swim	impaired ability to maintain position in water column
	equilibrium anomalies	inability to capture food
	loss of avoidance reaction	reduced escape reaction, increased susceptibility to predation
	Altered yolk utilization	
	reduced conversion efficiency	reduced biomass production, reduced larval size at time of first food intake, increased susceptibility to predation
	changed rate of yolk utilization	sshift in timing to first food intake
	Malformations	
	serrated fins	altered dermal respiration, swimming ability, susceptibility to disease
	eye defects (anophthalmia, microphthalmia, monophthalmia, cyclopia)	reduced visual perception, phototaxis, prey hunting ability
	mouth, lower jaw, branchial apparatus	impaired respiration, feeding success
	vertebral column	impaired swimming ability, escape reaction, prey hunting
Larvae (postyolk-sac)	Altered food relations	
	reduced food availability, conversion efficiency, growth	starvation; increased susceptibility to disease, predation; reduced survival potential at population level
	Reduced swimming capacity	increased susceptibility to predation
	Behavioral effects	
	changes in opercular rates coughing response	impaired gill function, respiration
Gonadal tissue	Success and timing of gamete production	desynchronization of spawning, larval production and food supply
	reduced fecundity	impaired reproductive success
	inhibition of maturation of ova	impaired reproductive success
	destruction of male germinal tissue	impaired reproductive success
	passage of contaminants through eggs to next generation	deleterious effects on offspring

the inlet and discharge canals to be 90 and 60%, respectively, when discharge temperatures were below 32 C. Above 32 C, survival dropped to about 30%. In general, survival after thermal shock depends on exposure time and previous temperature history (acclimation temperature), as shown by Hoss et al. (1974) for spottail pinfish larvae (*Lagodon rhomboides*). Subsequent sublethal effects could include increased susceptibility to predation in larvae shocked by passage through these systems.

Power plants also use chemicals to prevent marine fouling of their cooling water systems (Becker and Thatcher 1973), adding to the potential effects of thermal shock. Alderson (1972, 1974) found newly hatched larvae of plaice (*Pleuronectes platessa*) and sole (*Solea solea*) were less tolerant of free chlorine than the eggs. Growth of metamorphosed young of both species was markedly depressed at free chlorine concentrations near the LC50 level. Some held at 0.068 mg/liter chlorine showed evidence of gill damage.

Pollutional Environmental Changes

We now turn to sublethal effects of pollutants on marine and estuarine fish eggs, embryos, and larvae. In the following context, pollutants will be considered generally as substances added to the aquatic environment that have deleterious effects on living components of ecosystems. First, some examples of sublethal responses and their consequences are given in relation to observations of sex products or mature gametes, prior to fertilization.

Sex products — McGregor and Newcombe (1968), using mature trout sperm, reported on dose–response relations for low doses (25–400 rad) of ionizing radiation (1 rad = 10^{-2} J/kg). Treated sperm was used to fertilize normal eggs. Major eye malformations were observed in the resulting larvae. Malformations appeared to arise predominately as a result of chromosome aberrations induced in the mature sperm. Irradiation of either sperm or eggs also produced other gross abnormalities in the embryos and fry. Mann and Schmid (1961) subjected trout sperm to various detergents. Sperm motility was reduced at concentrations of 5–10 ppm, followed by reduced fertilization of eggs by the affected sperm. Fertilized eggs also were killed in 5 ppm dodecylbenzolsulphonate, a concentration of detergent that the authors indicated can be exceeded in polluted waters.

Eggs also may be subject to sublethal damage from exposure to chemical pollutants prior to fertilization. The authors (unpublished data) exposed Pacific herring eggs to different cadmium concentration–salinity-exposure time combinations prior to fertilization. Subsequently, a sequence of sublethal effects was observed throughout embryonic development. Fertilization virtually was unaffected by exposures up to 10 ppm cadmium prior to fertilization. Latent effects of cadmium preexposure became noticeable just prior to hatching, when near full-term eggs began to die. Reduction in egg survival was correlated directly with higher cadmium concentrations and longer preexposure times. Effects of preexposure to cadmium, then, were better determined at hatching rather than at fertilization. Preexposure to progressively higher cadmium concentrations resulted in progressively greater reduction in the volume of individual eggs, and this effect was intensified at longer preexposure intervals. Similarly, Braaten et al. (1972) fertilized Atlantic cod (*G. morhua*), Atlantic herring (*C. harengus harengus*), and plaice (*P. platessa*) eggs in various concentrations of by-products from production of vinyl chloride. There was no measurable effect on fertilization success caused by exposure to the chlorinated aliphatic hydrocarbons involved. However, higher concentrations (50 and 100 ppm) resulted in cessation of development of the plaice eggs in late stages of gastrulation. The origin of the sublethal response is not clear. In the herring egg study, cadmium apparently affects water intake and formation of the perivitelline space after fertilization. As the sperm were not preexposed to cadmium, the effects noted must have originated in the eggs. It is assumed that Cd^{++} competes with Ca^{++} for binding sites in the mucopolysaccharide "jelly" coat surrounding the capsule or zona radiata. Properties of either the jelly coat, the capsule, or both are assumed to have been altered so as to block entry of water or prevent its accumulation at the time of perivitelline space formation.

Effects of preexposure of Pacific herring eggs to cadmium were examined further by testing their bursting pressure at intervals after fertilization. Maximum bursting pressure of control eggs was achieved 20–50 h after fertilization, depending on the incubation salinity. In cadmium solutions (1.0–10.0 ppm Cd) at the same salinities, maximum bursting pressures occurred 100–500 h after fertilization. Eggs in 1.0–10.0 ppm cadmium appeared flaccid early in the incubation period, as though water hardening was delayed. Presence of calcium is known to be required for normal water hardening to occur. Presumably, cadmium–calcium interactions again were involved in altering the properties of the external membranes.

Differences in the rate of uptake of cadmium

may also be associated with species-specific differences (Dethlefsen et al. 1975) related to properties of the capsule, thickness of the jelly coat, egg surface to volume ratios and volume of the perivitelline space. In general, demersal eggs have thicker jelly coats, which tend to accumulate cadmium. For example, in Atlantic herring eggs, most cadmium contamination is found on the outer surface of the capsule (Rosenthal and Sperling 1974). Larvae from eggs exposed to cadmium after fertilization and formation of the perivitelline space contain much less cadmium. Some cadmium may enter the egg when water is imbibed to form the perivitelline fluid.

We conclude that short-term exposure of herring eggs to heavy metals, such as cadmium, can result in changes in properties of the external egg membranes. Further changes may occur if the contaminant is imbibed with water from the incubation medium at the time of water hardening. These changes are considered subethal responses; they can alter the organization of the egg so that a significant reduction in survival potential of the egg may occur at later stages of development.

Early embryonic development — There are two observations that should be mentioned first, which are well documented in the classical literature of developmental physiology. The first of these, noted in eggs undergoing merobastic cleavage, involves irregular cell divisions that result in an unusually high blastodisc of reduced diameter. Although such irregular cleavage patterns were described frequently in the older literature, we are not aware that this anomaly has been related quantitatively to situations involving external stressors. Recently we have noted such changes (unpublished data) in relation to cadmium and salinity levels in the incubation medium. The second type of observation relates to desynchronization of rates of blastodermal and periblast overgrowth of the yolk. Braum (1973) describes the effects of hypoxia on epiboly in Atlantic herring eggs. In eggs subjected to hypoxia prior to the fourth cell division, the periblast tends to migrate over the yolk considerably in advance of the blastoderm. In general, the normal progress of epiboly, described by Trinkhaus (1969) for *Fundulus* and by Devillers (1965) for salmonids, is altered under different stress situations. The consequences of these alterations are as yet largely unknown.

A number of other investigations have been concerned with the biochemical effects of pollutants and the manner in which they affect energy production and use in the fertilized egg and early embryo. These studies provide insight into recognition of the basic pathways an organism may follow in attempting to compensate for the presence of an environmental stress. The scope for compensation, however, is limited in the basic mechanisms involved; characteristically, the scope for compensation also changes as development proceeds.

Certain metabolic inhibitors, including the dinitrophenols, are decouplers of oxidative phosphorylation. They block phosphorylation of adenosinediphosphate (ADP), inhibiting the formation of adenosinetriphosphate (ATP). The latter of course is of central importance in metabolism. The presence of ATP in the living cell provides an ever-replenished store of chemical energy, a prerequisite for the occurrence of a multitude of metabolic processes. Resynthesis of ATP from ADP, therefore, is of decisive importance. It takes place along two different pathways, by phosphorylation through the substrate chain (glycolysis) or by the citric acid cycle. The action of dinitrophenol (DNP) is apparently that of altering the function of enzymes coupling phosphorylation to electron transport through the cytochrome system (Schatz 1967; Weinbach and Garbus 1969). Such compounds, while interfering with phosphorylation of ADP, have little or no effect on mitochondrial respiration.

In fish embryos, a decrease in cell ATP occurs under the influence of DNP, the amount of inhibition depending on the extent of blockage (Ishida 1951; Ishida et al. 1959: *Oryzias latipes*; Stelzer et al. 1971: *C. harengus harengus*). The embryo appears to try to compensate for reduction in ATP level, after a short period, by increasing its rate of respiration. The uncoupled respiration curves, at different stages of development, are similar. After an initial, rapid increase in rate, the curves drop and may achieve a level below that of the control, depending on the concentration of the inhibitor. However, the scope of the curves (difference between maximum of uncoupled rates and normal rates) decreases progressively in relation to the increasing base rate of normal respiration in succeeding embryonic stages.

Poisoning of fish embryos by DNP produces two types of responses, arrested differentiation and dedifferentiation. These responses may either be lethal or sublethal, depending on the strength and duration of the stress. Differentiation is taken to be the process by which cells alter their structure or function, developing new characteristics different from those of their initial condition. At lower concentrations of DNP differentiation may be retarded or arrested, as if the available energy budget is sufficient only for maintenance of cells in their current state of organization. At still higher concentrations, dedifferentiation may oc-

cur. That is, cells and tissues having reached a given stage of morphological or physiological organization may become altered, disorganized, or suffer disintegration. Even cells derived from different tissues may regress to acquire a similar appearance, in effect reverting to the appearance of undifferentiated cells.

Arrested differentiation has been noted in early embryos of *Clupea harengus harengus* (Rosenthal and Stelzer 1970; Stelzer et al. 1971). Embryos were subjected to DNP from epiboly, when the blastoderm was at the equator of the egg, until shortly before closing of the blastopore. Low concentrations of DNP arrested differentiation for periods of 5–7 days. Higher concentrations resulted in tissue dedifferentiation after several days of exposure.

Exposure of embryos to DNP at later stages of development produces many types of malformation. The spectrum of anomalies includes spiral twistings of the caudal region, defects of eyes and otoliths, malformation and partial dedifferentiation of individual organs and tissues, and finally, drastic dedifferentiation of the embryo (Rosenthal and Stelzer 1970). These anomalies are strikingly similar to the "spontaneous" malformations described in the literature (Mencl 1903, 1908; Tavolga 1949; Lutz and Lutz-Ostertag 1957), or those obtained using other environmental stressors. The latter include temperature shock (Stockard 1921: *Fundulus heteroclitus*), hypoxia (Alderdice et al. 1958: *Oncorhynchus keta*; Hamdorf 1961: *Salmo irideus*; Braum 1973: *C. harengus harengus*), heavy metals (Rosenthal and Sperling 1974: *C. harengus harengus*; Westernhagen and Dethlefsen 1975: *Platichthys flesus*; Westernhagen et al. 1975: *Belone belone*), oil dispersants (Lindén 1974: *C. harengus harengus*), "red mud" (Rotschlamm), a waste product of aluminum production (Rosenthal 1971: *C. harengus harengus*), and DDT and its metabolites (Dethlefsen 1975: *G. morhua, P. flesus, Pleuronectes platessa*). No anomalies were found that could be considered specific for the decoupling action of the dinitrophenols.

Leduc (1976) incubated newly fertilized eggs of Atlantic salmon (*S. salar*) in various concentrations of cyanide (0.01–0.10 ppm) until hatching. Cyanide principally inhibits cytochrome *a* of the electron transport system whereby substrate is oxidized and respiratory oxygen acts as the ultimate acceptor of hydrogen to form water. The cytochrome system and citric acid cycle generally are intimately associated, and poisoning of the former will interfere with energy production by the latter. Hatching success in all concentrations was reduced by 15–40%. During incubation, yolk to tissue conversion efficiency was reduced above 0.01 ppm HCN. Incidence of abnormalities increased (6–19%) with cyanide concentration (0.01–0.10 ppm). Deformations involved the head, eyes, mouth parts, and vertebral column. At hatching, exposed alevins generally were smaller than the controls ($\geqslant$0.04 ppm), although there was a rebound in most groups, conversion efficiency and growth increasing after hatching in the affected groups.

Struhsaker et al. (1974) applied various concentrations of benzene to eggs and to larvae after yolk exhaustion, of Pacific herring and northern anchovy (*E. mordax*). Eggs of the former were exposed initially at early cleavage, while the latter were in the gastrula stage. Exposure intervals in general were 24, 48, and 96 h. Exposed herring eggs showed lower survival at hatching, increased incidence of abnormalities, and delayed rate of development, particularly at higher benzene concentrations (35–45 ppm). Heart rate was also affected. Abnormalities included abnormal flexures of the vertebral column, monophthalmia, and incomplete lower jaw formation. Many resulting larvae were unable to swim or feed and eventually died. Responses of anchovy eggs were more variable. Some decrease in survival at hatching occurred, incidence of abnormalities increased, and yolk utilization in resulting larvae was delayed in higher concentrations (10.5, 24.0 ppm) and accelerated in lower concentrations (4.7 ppm). Rate of development after hatching was accelerated at lower concentrations; it was delayed at higher concentrations and older larvae were smaller. In general, direct mortality was fairly low in eggs exposed to benzene. However, the sublethal responses in early development produced numerous anomalies at hatching, which presumably would lower survival potential substantially in the resulting larvae.

The examples serve to demonstrate the general nature of the stress–stressor syndrome elicited by various pollutants. Regardless of the nature of the stressor the embryo appears to attempt to compensate for an energy deficit that it must overcome to continue living. During early embryonic development, energy levels are small but almost completely required for further differentiation. Stress, resulting from the presence of pollutants or changed levels of natural abiotic factors, would affect the rate or extent of cell of tissue differentiation at that time. Those malformations developing as a consequence may not be directly lethal. We consider them sublethal when they lead to reduced survival potential at subsequent levels of embryonic, individual, or population organization.

Effects of cadmium on enzyme activity provide another example of sublethal effects, effects im-

pressed at the level of cell metabolism but with significance in later stages of development. Mounib et al. (1975) found in Pacific herring eggs that exposure to 10 ppm cadmium results in decreased activity of four important enzymes. These include the (nicotinamide adenine dinucleotide) NAD- and NADP-malic enzymes, propionyl-CoA-carboxylase, and phosphoenol-pyruvate carboxykinase. In control eggs, phosphoenol-pyruvate carboxykinase activity increased by about two orders of magnitude in the period between the early blastodisc and the stage just prior to hatching. The increase is suggestive of the general importance of the enzyme in metabolism. In contrast, there was a substantial decrease in relative activity of the enzyme in cadmium-exposed eggs in the same period; activity of the enzyme was one third less than that of the controls. Relative activity of propionyl-CoA-carboxylase in the cadmium-exposed eggs was about 20% of the control level prior to blastopore closure and about 32% just prior to hatching. Relative activity of NAD- and NADP-malic enzymes remained stable during early differentiation, but was reduced by about 19% during the last stages of incubation, when embryonic growth is dominant with respect to differentiation. Since the enzymes studied are involved in biosynthetic processes, it is speculated that the depressive effect of cadmium on activity of the enzymes may explain why cadmium exposure results in smaller, inactive larvae at hatching.

Cadmium also provides an example of a more general type of response of eggs that may affect their survival potential at later stages of development. As mentioned earlier, cadmium affects water movement across the egg capsule. It alters their diameter and volume, hence their buoyancy. Eggs of a number of Baltic species are known to adjust their buoyancy in relation to the salinity of the external medium (Kändler and Tan 1965a, b: *G. morhua*, *Sprattus sprattus*, *Platichthys flesus*, *Limanda limanda*, *Enchelyopus cimbrius*, *Pleuronectes platessa*). Eggs of these species would occupy a position in the water column between the deeper, more saline (and frequently low-oxygen) waters of the Baltic and the surface layers that generally are much lower in salinity. Age of the eggs and both their volume and osmolarity are involved in these buoyancy adjustments. The evidence suggests that pollutants affecting egg volume and buoyancy, such as cadmium, could greatly alter the ability of eggs to maintain their location in the water mass. As cadmium reduces egg volume, the eggs likely would have a higher specific gravity and sink to lower, more saline, and frequently anoxic layers of water.

Advanced embryonic development — We now turn to sublethal effects noted in advanced embryos prior to hatching. Many of these will have been mentioned previously, having been initiated as a result of stress applied at early stages of development of the unfertilized or fertilized egg. In general, a number of morphological, physiological, or behavioral anomalies can be recognized. Some of these would have measurable influence on later survival; the implications of others are as yet unknown or uncertain. It also is difficult in some instances to distinguish clearly between morphological, physiological, or behavioral anomalies, as they are often related. For example, fin anomalies may be related to modified dermal respiration.

Lindén (1974, 1975) describes the effects of emulsifiers on heart rate in Atlantic herring embryos and larvae. One emulsifier was toxic at low (1 ppm) concentrations and produced marked reductions in heartbeat frequency at all concentrations (50–1 ppm) as well. Higher concentrations also increased apparent rates of dedifferentiation and embryonic malformation. The other emulsifier tested was much less toxic; it produced substantial but smaller reductions in heart rate at concentrations of 1000–25 ppm. However, in both cases, dedifferentiation, malformations, and heartbeat frequency were all more sensitive measures of total effect than were gross measures of survival from fertilization to hatching. It is perhaps significant that such emulsifiers may be used at high concentrations in restricted areas. Changes in embryonic heart rate also have been noted experimentally as a response to a variety of other pollutional stressors. These include DNP (Rosenthal and Stelzer 1970: *C. harengus harengus*), sulphuric acid from titanium dioxide production (Kinne and Rosenthal 1967: *C. harengus harengus*; Kinne and Schumann 1968: *Solea solea*), red mud from production of aluminum (Rosenthal 1971: *C. harengus harengus*), and cadmium (Westernhagen et al. 1975: *B. belone*).

Generally, at a stage of development after the embryonic axis is well established, muscular movement begins in the embryo. These movements involve slight body flexures or swimming motions, depending on the developmental state and specific pattern of behavior of the species in question. Embryonic movement is presumed to stir and circulate the perivitelline fluid, improving the distribution of oxygen to the embryo. In herring eggs exposed to pollutional stress, differences in embryonic muscular activity are clearly observable when the embryo has grown to encircle the yolk and the tail is past the head. Normal flexures of control embryos are largely replaced

by "shivering" or "trembling" movements in poisoned embryos. These movements involve rapid but limited muscular flexures and grossly resemble shivering movements in mammals. Normal, still more advanced embryos perform rotational movements of the whole body within the egg capsule (Holliday et al. 1964; Rosenthal 1966), whereas the shivering motions noted in early embryos continue in later stages of development (Westernhagen et al. 1974).

In some species, initial embryonic body movements are later replaced by a regular movement of the pectoral fins, which apparently serves the same purpose of circulating the perivitelline fluid. The frequency of fin beat increases with advancing embryonic development. Under the influence of some pollutants the frequency of fin movement is reduced (Westernhagen et al. 1975: *B. belone*). In *Belone*, pectoral fin activity is reduced in external cadmium concentrations below 5 ppm and completely depressed in 5 ppm cadmium. Fin beat frequency was also influenced by salinity of the incubating medium.

Larvae at hatching — Incubation time, the period between fertilization and 50% hatch, is lengthened at lower temperatures and lower dissolved oxygen levels. Low salinity may accelerate or retard hatching (Blaxter 1969), although, in general, the effect of salinity on developmental velocity appears rather minimal. Changes in time to hatch may or may not occur in eggs subject to pollutional stress throughout incubation. Byproducts of vinyl chloride production up to 100 ppm did not appear to influence developmental velocity in Atlantic cod, Atlantic herring, or plaice (*P. platessa*) (Braaten et al. 1972) nor did exposure to proteolytic enzyme affect incubation time of Atlantic herring eggs (Rosenthal and Mann 1973). However, exposure of similar eggs to cadmium shortened the incubation period by 1 (0.1 ppm Cd) to 5 (10 ppm Cd) days (Rosenthal and Sperling 1974). Similar findings were obtained for eggs of *B. belone* (Westernhagen et al. 1975) and *C. harengus pallasi* (unpublished data). The incubation period of Atlantic salmon eggs exposed to 0.08 and 0.10 ppm cyanide was lengthened 6 and 9 days (Leduc 1976).

Another frequently observed response to environmental stressors imposed during embryonic development is the emergence of smaller larvae at hatching. Reduced total length of newly hatched larvae has been reported for eggs incubated at supraoptimal temperatures, high salinities, or low oxygen conditions. Similar reductions have been noted for eggs incubated under the influence of pollutants including sulphuric acid, heavy metals, pesticides, red mud from aluminum production, and proteolytic enzymes.

The properties of the proteolytic enzymes contained in some detergent washing compounds are to some extent comparable to those of hatching enzymes. Their activity is related to pH and temperature. Rosenthal and Mann (1973) exposed Atlantic herring eggs to various temperature–salinity–proteolytic enzyme combinations. Under higher incubation temperatures and salinities, where enzyme activity is increased, larvae were smaller at hatching than in the appropriate controls. The effect was not a function of shorter incubation time and appeared to be a response to stress imposed throughout incubation. At incubation temperatures below 10 C, larval size at hatching was not influenced by the enzyme, even at the higher concentrations.

Dethlefsen (1974) incubated eggs of Atlantic cod, flounder (*Platichthys flesus*), and plaice (*Pleuronectes platessa*) in various concentrations of DDT. The resulting larvae were smaller at hatching, and size was related to concentration of DDT during incubation. Maintained in DDT-contaminated water, the larvae grew more slowly during the period of yolk absorption. Reduced swimming ability of smaller larvae at hatching may also reduce larval capacity to secure food and avoid predators. Ahlstrom (1954) reported that avoidance of nets by sardine (*Sardinops caerulea*) larvae was 15% greater in 7.5-mm larvae compared with 7.0-mm larvae. Similar behavioral and physiological changes may occur in salmonids exposed to DDT. Dill and Saunders (1974) exposed Atlantic salmon eggs to DDT (0.1–0.005 ppm) at gastrulation. Fish hatching from the 0.1 and 0.05 ppm exposures exhibited retarded behavioral development and impaired balance.

Numerous observations have been reported of structural and functional changes in larvae at and following hatching. Strictly speaking, they represent only the next stage in the sequence of events beginning with the earlier imposition of stress prior to or following fertilization. However, for the sake of convenience, those observations associated with yolk-sac larvae in particular are dealt with in the next section.

Yolk-sac larvae — Variations in size and shape of the yolk sac at and after hatching can occur in larvae previously exposed to various levels of natural abiotic factors or pollutants. By and large, few quantitative examinations of these variations have been attempted. Basically, yolk-sac size and shape varies in relation to incubation salinity and temperature conditions. At mean hatching time,

yolk-sac size in petrale sole (*Eopsetta jordani*) (Alderdice and Forrester 1971) is larger at higher salinities and higher temperatures. In Pacific herring (Alderdice and Velsen 1971), yolk sacs are larger at lower salinities and higher temperatures. Yolk sacs in *C. harengus harengus* are larger at lower salinities (Rosenthal and Mann 1973; Westernhagen et al. 1974) and appear to have a higher water content (Holliday and Blaxter 1960). Yolk sacs of flathead sole (*Hippoglossoides elassodon*) (Alderdice and Forrester 1974) appear reasonably constant in size at various incubation salinities, but are smaller at higher temperatures. In biardiella (*Biardiella icistia*) yolk-sac size is largest at hatching in lower temperatures (21 C) and lower salinities (20‰) (May 1974). However, volume definitely was related to water content; dry weights of larvae at hatching were highest at lower temperatures (21, 24 C) and intermediate salinities (30‰). Dry weights of larvae at yolk exhaustion were highest at similar temperatures but lower salinities (20‰), and yolk utilization efficiency was highest at 24 C, 20‰. May's results also support the contention that optimum conditions for egg and larval development may differ, particularly in this instance with regard to salinity. These variable responses currently are difficult to explain fully. They can of course reflect differences in rate of energy utilization (Blaxter and Hempel 1966), as well as changes in water content of the yolk sac in relation to osmotic concentration of the surrounding medium. We suspect from current studies (unpublished data) that species-specific ranges of tolerance are involved, and that the extent and direction of change of incubation conditions from species-specific optimal environmental conditions (e.g. salinity, temperature, dissolved oxygen) are also associated with determination of yolk-sac volume.

Complexities in yolk-sac size and shape, alluded to in regard to natural abiotic factors, increase when eggs also are subjected to pollutional stress during incubation. Rosenthal and Mann (1973) found differences in yolk volumes among their Atlantic herring larvae from eggs incubated under various salinity–temperature–proteolytic enzyme combinations. With increasing enzyme concentration, yolk-sac size was reduced substantially in larvae from the higher salinity–temperature incubations. In Atlantic herring (Westernhagen et al. 1974), yolk-sac volume increased in higher cadmium concentrations, particularly in lower incubation salinities. We have found similar increases in yolk-sac size in Pacific herring (unpublished data) larvae from eggs incubated in 0–10 ppm Cd. Associated with these observations was an earlier, apparently impeded movement of water across the egg capsule. The effect was noted in particular when eggs were transferred to higher salinities (35‰).

We now turn to a consideration of observations and implications arising from the presence of deformities in hatched larvae. Malformations, resulting from environmental stress, may play roles of minor to major importance in relation to survival potential of a larval population. In general, malformations observable after hatching that originated from tissue injury during earlier stages include 1) yolk-sac deformities, including patches of necrotic tissue and incomplete yolk circulation; 2) various types of eye deformation, generally involving reduction in size of one or both eyes, and as well, disorganization of retinal tissue; 3) otic capsule defects, ranging from missing otoliths to absence of otic capsules; 4) jaw anomalies, including stages from absence of the lower jaw to its deformation or delayed formation; 5) fin defects; and 6) malformations of the vertebral column. Some of these have obvious effects on survival. Some may have subtle but important consequences. In others, the possible significance of noted effects in relation to survival potential is not well understood.

Yolk-sac deformities have occurred in Atlantic herring larvae as a result of exposure of eggs to crude oil fractions in sea water (Kühnhold 1969). Others have been noted after X-ray irradiation of rainbow trout (*Salmo gairdneri*) (Bühringer 1973), and after exposure of Atlantic herring eggs to DNP (Rosenthal and Stelzer 1970). Such deformities might or might not alter yolk utilization efficiency and early larval growth. Spontaneous rupture of the yolk-sac is often observed also as a result of exposure to low boiling point fractions of crude oil in sea water, an injury that could occur after hatching but greatly reduce the individual's chances for survival.

Eye deformities occur commonly as a result of stress imposed during incubation. Anophthalmia, bilateral microphthalmia, and dedifferentiation of optic anlage have been noted in Atlantic herring larvae from eggs exposed to DNP (Rosenthal and Stelzer 1970). Similar types of injury occur in plaice and rainbow trout eggs exposed to x-radiation (Ward et al. 1971: *P. platessa*; Welander 1954; Bühringer 1973: *S. gairdneri*). In Pacific and Atlantic herring eggs exposed to cadmium, there is a reduction in eye diameter in newly hatched larvae (unpublished data: *C. harengus pallasi*; Westernhagen et al. 1974: *C. harengus harengus*), particularly at higher concentrations (>1.0 ppm Cd).

Otic capsules and otoliths also are smaller in

larvae from eggs incubated in cadmium solutions, the extent of reduction depending on the cadmium concentration (Westernhagen et al. 1974: *C. harengus harengus*). At 5 and 10 ppm cadmium the larvae often hatch without otic capsules. In both Atlantic herring and in Pacific herring (unpublished data: *C. harengus pallasi*), reduction in otic capsule size begins at a concentration of about 1 ppm cadmium. In the latter species, at 10 ppm cadmium, usually both otoliths were missing; less frequently one or both otic capsules were unformed. Cadmium appears to interfere with utilization of calcium, required in formation of the otoliths and otic capsules. The malformation is of particular interest relative to survival of affected larvae. Such larvae are unable to maintain equilibrium during swimming, even though they otherwise appear completely normal. Unable to perform normal swimming movements, these larvae would be unable to maintain location in their environment. Furthermore, they would not be able to learn and perform prey-capture manoeuvres required for successful feeding and growth. The consequences of the malformation would include increased susceptibility to predation and eventual death from starvation, once the yolk is utilized and the "point of no return" is reached.

Anomalous formation of the lower jaw was mentioned earlier as a malformation resulting from exposure of eggs to limiting levels of natural environmental factors. Circumstantial evidence suggests similar anomalies may occur in early development through exposure of eggs to pollutants, although the evidence is not too clear. Jaw and other anomalies (head, pectoral and pelvic girdles, opercules, vertebral column) occur widely among estuarine fishes on the Atlantic coastline from Massachusetts to Texas, particularly in the more northerly waters (Kroger and Guthrie 1973). The open-jaw syndrome of salmonids (Crouch et al. 1973: *Oncorhynchus, Salmo*) seen in hatchery juveniles may be of genetic origin or may result from exposure to environmental or pollutional teratogenic influences. In this instance, the lower jaw is significantly shorter than normal and is dislocated; it bears a striking resemblance to jaw deformities noted in herring larvae incubated at limiting temperature–salinity conditions (Alderdice and Velsen 1971). Jaw anomalies, among others (head, eyes, limbs, sternum, urogenital system), have been produced experimentally in mammals and birds exposed to various substances during early embryonic development (Landauer and Naseem 1973; Kato and Kitagawa 1974; Puget et al. 1975). The teratogenic substances included a number of compounds that would likely interfere with pyridine nucleotide utilization through stereochemical mimicry. Crouch et al. (1973) noted that jaw abnormalities interfered with feeding ability in hatchery fish. In the natural environment such anomalies likely would lead to reduced food-capture ability for continued growth and survival.

Deformation of fins is reported frequently as a result of stress imposed during incubation. Newly hatched larvae of *Belone belone* exhibited serrated or frayed fin folds and caudal fins after incubation of the eggs in 1 ppm cadmium (Westernhagen et al. 1975). Kühnhold (1972) reported anomalies in the fin folds of newly hatched larvae of Atlantic cod, Atlantic herring and plaice (*P. platessa*) exposed to crude oil dispersants in sea water. Serrated fins would affect swimming performance, and injury to the fin fold could also affect cutaneous larval respiration. Respiration of normal, early plaice (*P. platessa*) and Atlantic herring larvae seems fairly independent of oxygen level in the surrounding medium (De Silva and Tytler 1973). Ultramicroscopic corrugations on the epidermis of larval Atlantic herring, sardine (*Sardinops caerulea*) and plaice (*P. platessa*), described by Lasker (1963), Jones et al. (1966), Lasker and Threadgold (1968), and Roberts et al. (1973), may serve as a means of increasing surface area for cutaneous respiration. Damage to cutaneous respiratory surfaces could have serious consequences, as functional gill filaments may be absent in newly hatched larvae. In Atlantic herring, the filaments do not appear until the young fish reaches a length of about 20 mm, some weeks after hatching (Harder 1954).

Injury to the vertebral column or its anlage, as a response to environmental stress, is commonly seen by most investigators working with fish eggs and larvae. The range of anomalies is extensive, from slight, single flexures of the vertebral column to multiple spiralling and partial dedifferentiation (Rosenthal and Stelzer 1970). Some elements of the trunk may fail to form, depending on the nature of the stressor and its time of application during embryonic differentiation (Alderdice et al. 1958; Garside 1959). Such deformities may occur as a result of exposure to extremes of temperatures, salinity and dissolved oxygen concentration, or to radiation and various pollutants. Larvae hatched from eggs of *B. belone*, subjected to cadmium during incubation, exhibited vertebral column flexures, reduced activity and swimming ability (Dethlefsen et al. 1975). Those exposed to concentrations below 2 ppm tended to recover as they fed and grew in uncontaminated water. Those incubated at levels of 2 ppm cadmium or more survived to the end of the yolk-sac stage but were unable to feed and

died shortly thereafter. The consequences of such malformations of course depend upon their severity. If activity and swimming ability are reduced, increased risk of starvation or predation would be anticipated, leading to reduced survival potential of the affected individuals.

In the previous section we have discussed responses to stress imposed on embryonic stages that may have a deleterious influence on resulting abnormal larvae after hatching. These influences, in general, would lower the individual's capacity for normal activities, thereby diminishing behavioral capacities associated with food gathering and avoidance of predators. In line with our conceptualization of sublethal effects, environmental stress may also be imposed on normal larvae after hatching, resulting in similar, reduced survival potential later in development beyond the yolk-sac stage. Such posthatching encounters with stressors are considered here. Kühnhold (1969) reported reduced swimming ability in newly hatched Atlantic herring larvae exposed to different concentrations of crude oil in sea water. Depending on concentration and type of oil used, activity patterns changed to uncoordinated movements, and total activity was reduced substantially within 2 days of the start of exposure. Mironov (1972) reported that newly hatched larvae of *Rhombus maeoticus* exposed to oil extracts, became immobile and sank immediately. Reduced swimming ability has been observed by other investigators, including Dethlefsen et al. (1975) working with DDT and Atlantic cod larvae, and by Rosenthal and Sperling (1974) and Westernhagen et al. (1974) working with cadmium and Atlantic herring larvae. In the latter instance, larvae gradually became immobile in concentrations of 2–3 ppm cadmium. Wilson (1972), using herring larvae, found that <3 ppm of an oil dispersant was the approximate toxic limit. Under the influence of the dispersant, first food-capture maneuvers were impaired. Wilson (1974) also studied avoidance behavior of herring and plaice (*P. platessa*) larvae influenced by oil emulsifiers. The emulsifiers were not avoided and produced narcotic effects within 20 min of exposure. Recovery times from narcosis were relatively long. Under the experimental conditions, larvae in the upper contaminated waters became narcotized, sank into cleaner water, recovered, then swam upward again into the dispersant-containing layer. Using herring larvae, Rosenthal and Gunkel (1967) found that high concentrations of oil emulsifier in sea water produced "flight reactions." Low concentrations (≤2.5 mg/liter) produced disturbances of equilibrium and associated swimming behavior. It also has been demonstrated that anesthetized larvae are more susceptible to predation. One would conclude from the foregoing observations that normal larvae subjected to the action of some pollutants would have difficulty maintaining position in a water mass, would feed less efficiently, and be more subject to predation.

Effects of benzene in sea water were investigated by Struhsaker et al. (1974) using larvae of Pacific herring and northern anchovy. Normal larvae were exposed to various concentrations after yolk exhaustion. Exposure at first produced erratic swimming, lethargy, and reduced swimming and feeding activity. At lower concentrations, larvae appeared to recover in 2–3 days. In general, exposure to 17.7 ppm or greater concentrations reduced survival, decreased food intake, increased rate of respiration, and resulted in smaller larvae. Development was delayed in higher concentrations and accelerated at low (5–10 ppm) concentrations. Anchovy larvae exposed to benzene at yolk exhaustion were inactive, development rate was reduced, and larvae were smaller. In both instances, the larvae after hatching seemed more sensitive than eggs to lower concentrations of benzene. Mortality was low, and most larvae eventually seemed to recover, but food intake was lowered and growth rate retarded.

Pollutional conditions that affect food supply and feeding behavior may also reduce the survival potential of larvae. Laurence (1974) showed that unfed larvae of largemouth bass (*Micropterus salmoides*) had lower swimming speeds than fed larvae. Swimming capacity determines the water volume a larva may search per day (Rosenthal and Hempel 1970; Blaxter and Staines 1971; Hunter 1972). Therefore, starving or unfed larvae may have less chance of finding food sufficient for growth and continued survival. Rosenthal (1971) also found that "red mud" particles in suspension had an unexpected effect on Atlantic herring larvae. Particles of red mud, taken in while larvae were swimming, lodged in and blocked their gullets. Larvae made prey-capture manoeuvres, but were unable to swallow captured prey.

Pollutants may reduce food availability, resulting in starvation and death of larvae indirectly. Responses associated with these sublethal effects of food deprivation are more difficult to ascertain. The period between yolk utilization and transition to exogenous sources of food must be a critical one for many species; yet, the relationship remains unclear in many instances. Some possible, associated effects have been identified. They include changes related to larval condition, such as levels of total activity and food-capture behavior at various stages of yolk utilization (Rosenthal

1969; Alderdice and Velsen 1971), changes in tissue water content relative to extent of food deprivation (Ehrlich 1974), increases in intracellular space and decrease in cell size (Love et al. 1968), and changes in tissue water content, sinking rate, and activity (Blaxter and Ehrlich 1974). Condition factors of field-caught larvae have been investigated extensively (Hempel and Blaxter 1963) in an attempt to correlate them with recruitment success. So far, no clear relation has been shown between larval condition and survival potential of the population. On the other hand, weak, undernourished larvae may be eliminated quickly under field conditions and provide little real evidence of their numbers in plankton samples. Potential sublethal effects of malnutrition remain an open question. In general, the ecology of fish larvae in relation to food supply in polluted waters has yet to be elaborated.

Gonadal tissue — Action of pollutants on gonadal tissue provides clear examples of sublethal effects. Contaminants can reduce the fecundity of the spawning population, lower the survival potential of the young actually produced, and thereby limit the numerical size of the succeeding generation. Goldfish (*Carassius auratus*) injected with cadmium (Tafanelli and Summerfelt 1975) showed destruction of male germinal epithelium and reduced production of sperm. Production of ova was either retarded or inhibited. Other histopathological changes in the goldfish likely would increase susceptibility to disease and reduce tolerance to environmental change. Sangalang and O'Halloran (1972) also found testicular damage in brook trout (*Salvelinus fontinalis*) exposed to nonlethal doses of cadmium down to 0.01 ppm. Inhibition and degeneration of gonadal tissue resulted from exposure of the guppy (*Lebistes reticulatus*, Crandall and Goodnight 1962) to 2–5 ppm lead nitrate over a 4-mo period. Complete inhibition of spawning resulted from exposure of fathead minnows (*Pimephales promelas*) to 0.07 toxic units of copper (Mount 1968); egg production in the same species was almost completely eliminated at 0.035 ppm of zinc (Brungs 1969). Sprague (1971) reviewed a number of instances where DDT from contaminated parent fish, transmitted through yolk lipids, caused problems in the young hatching from the contaminated eggs. These include mortality of fry (Burdick et al. 1964, 1972; Allison et al. 1964; Macek 1968) and increased sensitivity to DDT in the fry (Holland et al. 1966). Anderson and Everhart (1966) associated average DDT residues of 0.87–6.0 ppm in gonads of Sebago Lake Atlantic salmon with a decline in the sport fishery. Others have found that egg production in trout fed sublethal doses of DDT was not lowered. However, high mortalities occurring in the eggs were correlated with DDT levels accumulated in the eggs.

DeCew (1972) tested the toxicity, efficacy and teratogenicity of mixtures of antibiotics used to control disease in chinook salmon (*O. tshawytscha* prior to spawning. Some combinations of levels of penicillin G procaine, dihydrostreptomycin, and oxytetracycline-HCl increased the frequency of teratogenic anomalies in fry hatched from eggs of treated fish. These deformities included foreshortened mandibles, narrow caudal fins, and shortened anal fins.

Experiments by Dethlefsen (1974) have shown that concentrations of DDT influencing survival of Atlantic cod, flounder (*Platichthys flesus*), and plaice (*Pleuronectes platessa*) larvae are in excess of those usually found in sea water. Danger of acute impairment of embryos and larvae would be relatively low from exposure to natural levels during incubation. Of more concern, however, is the fact that low environmental concentrations can lead to high tissue concentrations by bioaccumulation. Smith and Cole (1973) exposed adult winter flounder (*Pseudopleuronectes americanus*) to nonlethal concentrations of DDT. Eggs spawned from those adults showed abnormal gastrulation. There also was a high incidence (39%) of vertebral deformities in newly hatched larvae, including bone erosion and hemorrhaging at vertebral junctures. DDT concentrations in the eggs ranged between 0.39 and 4.60 ppm; the controls contained 0.11–0.57 ppm DDT. Concentrations of 2–4 ppm DDT often are found in gonads of cod from the North Sea and Baltic Sea (Huschenbeth 1973). Therefore, during oogenesis rates of accumulation of DDT, based on the trace levels observed in the environment, could produce gonadal concentrations sufficient to affect survival potential of the species through lowered viability of the fertilized egg and later larvae.

Discussion

From the available experimental evidence on marine eggs and larvae, it seems certain that a growing number of cause–effect relationships will be detected that fit the definition of sublethal effects. At the cell tissue, and individual level, detection of mechanisms initiating sublethal responses undoubtedly will be strengthened by biochemical enquiry. Similarly, the consequences of sublethal response should become better recognized through histological, morphological, physiological, and ethological enquiry.

Nevertheless, a substantial gap remains between inferences based on observed individual responses and the implications they generate regarding the

cellular level at which they were elicited on the one hand and their effect on survival potential of the population on the other hand. Frequently at the population level either the potential cause is known and the probable effect is inferred, or the effect is observed and the probable cause is unknown or implied. Ecological surveys of polluted habitats (Sprague 1971) could provide insight into such problems. Yet, that course of action is disquieting if the loss of natural ecosystems is the price paid for the promise of better understanding of these problems.

Probably most shifts in environmental conditions produce some perturbations in ecological structure, whether induced by natural or man-made changes in natural abiotic factors, by pollutional changes, or by both. Basically, when environmental alteration reduces survival potential of aquatic populations, we are faced with the need to comprehend the cause-and-effect mechanisms involved. We believe attention should be directed toward two basic concerns.

1) Current pollution research appears to be focused primarily on monitoring programs which collect information on residue levels in the environment.

2) Methods of assessing the dangers of environmental change seem largely to have become fixed within a technology that measures or draws inferences from lethal effects.

We believe that more effort needs to be expended in determining the biological implications of environmental changes and pollutant residues in aquatic ecosystems. Further, we strongly suggest the need for an expanded and more unified enquiry into sublethal effects, at individual and population levels, by such means as those suggested in this survey. Finally, we suggest the need for a strong association between monitoring effort and enquiry into sublethal effects in the search for better means of achieving an intelligent balance between man's use of the environment and the need to sustain healthy aquatic ecosystems.

It is encouraging to recognize that the ultimate effects of the broad variety of stressor–stress systems reviewed may be traced back to a more limited array of organismic responses, often appearing to involve similar physiological and biochemical compensatory mechanisms. It would seem from this review that most sublethal effects are biochemical in origin, that they are expressed as histological, morphological, physiological or ethological responses, and that these responses alter the population structure through integration of associated changes of individual survival potential. Within this framework it would seem that the ultimate tactical manoeuvre of an egg is to remain alive, whatever the cost, as long as the organism's compensatory apparatus is not flooded or overwhelmed by the imposed stress. Hence, the cost, though nonlethal at the time of stress compensation, ultimately may result in mortality in another, later stage of development. Thus, the organism trades certainty of death at one stage for a lower probability of survival at a later stage.

Bartholomew's concept that biological mechanisms, reacting to stress, elicit sublethal responses with ecological consequences, remains challenging and attractive, but in need of more extensive investigation. From this viewpoint and on the basis of the evidence reviewed, we conclude that:

1) Sperm and eggs released into the marine environment are sensitive to a variety of pollutants, even at low concentrations and short exposure times.

2) The fertilized egg is well protected against those pollutants for which the capsule and jelly coat act as a barrier to penetration (heavy metals, proteolytic enzymes of washing compounds). Nevertheless, such protection may be diminished if perivitelline fluid formation takes place after fertilization in a polluted medium and pollutant enters the egg along with imbibed water.

3) Notwithstanding the protective action of the capsule, changes occur in the properties of the egg coverings, leading to secondary sublethal effects (interference with water hardening). Yet, concentrations of pollutants producing these effects in most cases seem to be in excess of those observed in nature (cadmium).

4) The fertilized egg, on the other hand, is highly sensitive to those compounds that interfere with intermediary metabolism and energy production, and for which the external coats do not act as an effective barrier (DNP).

5) After hatching, larvae are very sensitive to many pollutants as shown by the immediate occurrence of altered responses and rapid uptake of pollutants.

6) Exposure of adult fish to low concentrations of various pollutants, including radiation, can have significant effects on gonadal tissue. Some pollutants are bioaccumulated to significant levels in ovarian tissue. Effects are expressed in the next generation with respect to fertilizability of affected eggs, embryonic development and teratogenetic anomalies, survival to hatching, and successful posthatching development.

7) Available data suggest that several stages in the life cycle of marine fishes are more susceptible to environmental and pollutional stress. These are a) gonadal tissue, b) the highly plastic early embryo, and c) the stage of larval transition between reliance on endogenous and exogenous sources of food.

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Basket Traps for Surveys of a Gammarid Amphipod, *Anisogammarus confervicolus* (*Stimpson*), at Two British Columbia Estuaries

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LEVINGS, C. D. 1976. Basket traps for surveys of a gammarid amphipod, *Anisogammarus confervicolus* (*Stimpson*), at two British Columbia estuaries. J. Fish. Res. Board Can. 33: 2066–2069.

Basket traps filled with *Fucus distichus*, a fucoid alga, were used for assessing the distribution of a gammarid amphipod, *Anisogammarus confervicolus*, at the Squamish and Cowichan river estuaries in southwestern British Columbia. Over a 17-day period amphipods accumulated in baskets at an exponential rate. Compared with quadrat sampling, basket samplers yielded biomass data more quickly. Distribution patterns determined by quadrat and basket sampling at low tide were similar, but data obtained by the basket samplers may be more useful as they integrate abundance over numerous high tide periods.

LEVINGS, C. D. 1976. Basket traps for surveys of a gammarid amphipod, *Anisogammarus confervicolus* (*Stimpson*), at two British Columbia estuaries. J. Fish. Res. Board Can. 33: 2066–2069.

Nous avons employé des casiers remplis de *Fucus distichus*, une algue fucoïde, pour établir la répartition d'un amphipode gammaride, *Anisogammarus confervicolus*, dans l'estuaire des rivières Squamish et Cowichan dans le sud-ouest de la Colombie-Britannique. Sur une période de 17 jours, les amphipodes se sont accumulés dans les casiers à un taux exponentiel. Comparativement à l'échantillonnage par quadrats, l'échantillonnage au casier fournit des données sur la biomasse plus rapidement. Les deux méthodes d'échantillonnage donnent des distributions semblables, mais les données provenant de l'échantillonnage au casier peuvent être plus utiles parce qu'elles renseignent sur l'abondance durant plusieurs périodes de haute marée.

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ESTUARINE, intertidal habitats in British Columbia are in demand for industrial purposes because flat land at tidewater is in short supply. Conflicts arise because the estuaries are utilized by commercially significant fish, including juvenile salmonids (*Oncorhynchus* spp). One of the common organisms in salmon stomachs from estuarine environments in British Columbia is the gammarid amphipod, *Anisogammarus confervicolus*: (Levings 1973). There is great spatial variability in habitats of most estuaries, so it is difficult to obtain comparable, quantitative samples of organisms such as amphipods. However, such data are necessary to assess the biological significance of specific areas.

This note reports a method developed to assess the distribution of *A. confervicolus* in estuaries, using basket traps filled with *Fucus distichus*, a fucoid alga. Two subspecies of *F. distichus* are reported from British Columbia (Nassichuk 1975; see also Widdowson 1973) but the alga was not identified to the subspecific level in the present study. Basket samplers filled with artificial substrates, such as crushed limestone (e.g. Kreis et al. 1971), have been used to sample invertebrates in lakes and rivers, but there are no previous reports of use in estuaries. In this report, some results of assessments at the Squamish (49°41′N; 123°10′W) and Cowichan river (48°45.5′N; 123°38.5′W) estuaries are presented.

Materials and field procedures — The wire baskets utilized in the assessment work were of the following dimensions: 20.3 × 34.3 × 22.8 cm with square mesh of 1.9 cm each side. The diameter of the wire was 2.6 mm and it was composed of ungalvanized steel (99.5% iron). The wire baskets will rust if left in place for long periods, but stainless steel, vinyl-

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coated wire, or plastic could be used. These materials would of course add to the cost of the samplers.

Fucus appeared to be the best material for filling the baskets, compared to crushed rocks (2–5 cm diam) and shavings of polyvinyl chloride (PVC) (the latter material was tested by Mr J.-B. Coustalin). The crushed rock attracted amphipods but the baskets were too heavy for convenient manipulation and amphipods were often damaged by rocks. The PVC ribbons were also suitable but had to be obtained by peeling the material from PVC piping with a lathe, which was a very laborious procedure. *Fucus* is a very common and abundant alga on the British Columbia coast, and so is readily available for filling the basket samplers. By washing the alga on a large mesh (1 cm) screen, all organisms living in the *Fucus* were easily removed before filling the baskets and starting a survey. The alga was loosely packed in the baskets which each held approximately 2 kg wet wt *Fucus*, equivalent to approximately 360 g dry wt. Small baskets each holding about 85 g dry wt. *Fucus* were used in an experiment to determine colonization time.

When baskets were retrieved at low tide, *Fucus* from each basket was emptied into plastic bags and returned to the laboratory. *Anisogammarus confervicolus* was then separated from *Fucus* by washing through a series of screens (10 mm. 1.0 mm, and 0.5 mm). The dry weight of *Fucus* and *A. confervicolus* in each basket was obtained after drying the alga and amphipods at 100 C for 48 h. At the Cowichan estuary, a number of organisms other than *A. confervicolus* (e.g. isopods, *Pentidothea* spp.) colonized the baskets, so detailed sorting was necessary.

The baskets were suspended from posts, logs, and other structures at approximately 2.5 m above chart datum. At low tide, *A. confervicolus* is most abundant at this elevation (Levings 1973). Pairs of baskets were suspended at a number of sites in the estuaries (Fig. 1) and left in place for 10–14 days. At Squamish, the tests were carried out in May and June 1975. Since previous studies (Levings 1976) showed that *A. confervicolus* is most abundant in spring, the sampling took place when amphipods were numerous and widespread. Tidal fluctuations in May and June ranged from 0 to 4.5 m so the baskets were out of the water approximately half the time. At the Cowichan estuary, sampling occurred in late September 1975 when changes in tidal amplitude were slightly less marked.

Data from quadrat samples at low tide were obtained at sites corresponding to sites where baskets were suspended. Five replicate quadrats (0.25 m^2 or 0.06 m^2) were obtained at random locations within an area of approximately 25 m^2. Sediments and biota were collected by scraping the substrate within the quadrats with a trowel (depth 2 cm). The samples were washed through a 0.5-mm sieve and preserved in 10% formalin. In the laboratory, amphipods were removed from sediments using an elutriation technique and further sorted using a microscope at 12× magnification. At Squamish, surface plankton tows at high tide were completed (May 27, 1975) with a

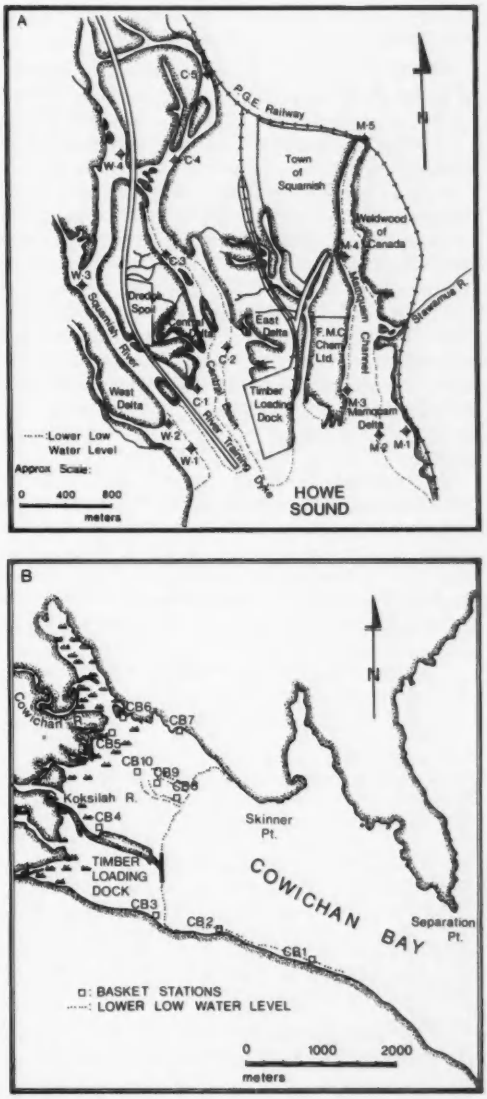

FIG. 1. Squamish (A) and Cowichan (B) estuaries showing locations where baskets were suspended.

SCOR/UNESCO net (0.25-m^2 surface area; 350-μ mesh size) at locations close to the basket sites. The length of each plankton haul was approximately 30 m.

An experiment to determine the rate at which amphipods colonized the *Fucus* was carried out at Squamish. Five pairs of baskets were suspended on a rope stretched between two posts (Station C1; Fig. 1). The pairs of baskets were suspended every

3 m and retrieved at random at 3- or 4-day intervals over the period September 19–October 6, 1975.

Results — Amphipods accumulated in baskets at an exponential rate (Fig. 2). Presumably the "carrying capacity" of individual baskets would eventually be reached, but this level was not achieved in 17 days.

At the Cowichan estuary, the sample sites were chosen to test for differences in the abundance of *A. confervicolus* between stations adjacent to the river mouths (stations CB4–CB10) and sites further removed from the influence of fresh water (stations CB1–CB3). Mean amphipod biomass was <1 mg g^{-1} *Fucus* at the latter stations and approximately 2 mg g^{-1} *Fucus* at the locations closer to the river mouth (Table 1). Biomass differences were significant, as judged by a *t*-test ($t = 3.60$; df = 9; $P < 0.01$) (Steel and Torrie 1960).

In the initial assessment tests at Squamish, *A. confervicolus* accumulated in the basket samplers in amounts ranging from 0 to 150 mg g^{-1} *Fucus* (Table 1). A subsequent survey was designed to test for differences between the three major channels, namely the Squamish River (stations W1–W4), the Central Basin (stations C1–C5), and the Mamquam channel (stations M1–M5) (Table 1). Amphipod biomass did not differ significantly between the channels as determined by an analysis of variance ($F = 1.96$; df = 2, 24; $P > 0.05$) (Steel and Torrie 1960). The mean abundance of amphipods in the baskets at the various channels was as follows (mg g^{-1} *Fucus*): Squamish River, 22.8 (SD = 55.3); Central Basin, 53.5 (SD = 48.8); and Mamquam Channel, 26.6 (SD = 48.1).

At Cowichan, quadrat sampling for amphipod biomass at sites adjacent to the basket locations showed the same distributional patterns as the basket samplers. The biomass of *A. confervicolus* at the "marine" sector of the Cowichan estuary (stations CB1–CB3) was <1 mg dry wt 0.25 m^{-2}, compared to 3 mg dry wt 0.25 m^{-2} at stations closer to the river mouths (stations CB4–CB7). This difference was statistically significant as determined by a *t*-test ($t = 10.8$; df = 29; $P < 0.01$). At the Squamish estuary, previous quadrat sampling under various types of cover material (sedge rhizomes, *Fucus*, bark, wood debris) has shown that amphipod biomass is

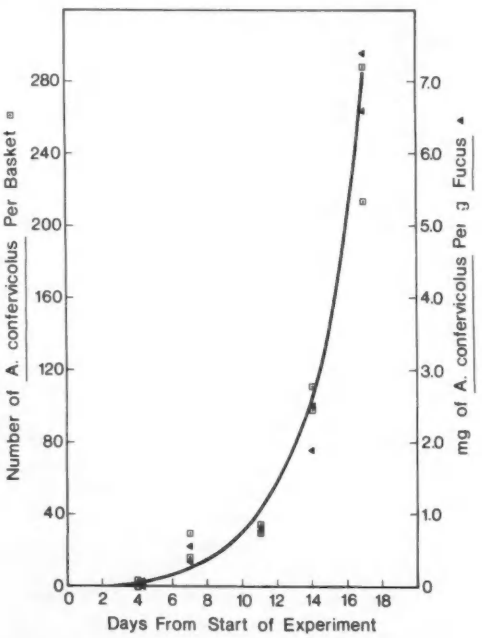

FIG. 2. Accumulation of *Anisogammarus confervicolus* (biomass and numbers) over time at Station C1, Squamish River estuary. The fitted regression line, converted from a semilogarithmic regression, is shown for numerical data.

TABLE 1. Accumulation of *Anisogammarus confervicolus* biomass (milligrams *A. confervicolus* per gram *Fucus* dry weight) in replicate basket samplers at the Squamish and Cowichan estuaries, 1975. ns = indicates no sample obtained.

Stn.	mg *A. confervicolus* g^{-1} dry wt. *Fucus*
	Apr. 29–May 12 — *May 15–28*
C1	35, 27 — 1, 2
C2	12, 17 — <1, 3
C3	26, 40 — 90, 53
C4	22, 21 — 99, 132
C5	ns — 80, 74
W1	ns — 0, ns
W2	ns — 0, 10
W3	ns — 0, 148
W4	ns — 1, 1
M1	ns — 31, 20
M2	ns — 2, 150
M3	ns — 1, ns
M4	ns — 2, 2
M5	ns — 0, 32
	Sept. 17–30
CB 1	ns, <1
CB 2	<1, <1
CB 3	<1, 0
CB 4	1, 2
CB 5	7, 4
CB 6	<1, <1
CB 7	1, 4
CB 8	0, 0
CB 9	5, 5
C 10	1, 7

relatively uniform across the estuary (seaward portion), but cover material is restricted on the West delta owing to flushing by river currents (Levings 1976). Data obtained in May 1973 showed amphipod biomass was as follows at the four delta sectors: (milligrams dry weight 0.06 m^{-2}): West, 120 SD = 157); Central, 105 (SD = 162); East, 171 (SD = 364); and Mamquam, 367 (SD = 366). There was no significant difference in biomass between the sampling areas, as judged by an analysis of variance ($F = 1.88$; df = 3,37; $P > 0.05$). However, the relative lack of cover material on the West delta implies that fewer amphipods can utilize West delta habitats at low tide.

Plankton net sampling yielded very few amphipods (maximum 2 mg dry wt m^{-3}) at all stations at Squamish.

Discussion — Distributional patterns of *A. confervicolus* can be determined much more rapidly with the basket samplers compared to quadrat sampling. Sample sorting from quadrats was at least twice as time-consuming as working with material collected in the basket samplers.

Because the basket samplers attract *A. confervicolus* that are drifting at high tide, biomass data obtained are a good reflection of the quantity of amphipods available for juvenile salmonids. At low tide, amphipods accumulate under diverse cover material, and evaluation of habitats at low tide (quadrat sampling) presents serious sampling problems and may provide incorrect information pertaining to sites where the amphipods are utilized as fish food. For example, at Squamish, sedge (*Carex lyngbyei*) rhizomes overhanging embankments are a primary habitat on the seaward portion of the Central and East deltas. However, catches of juvenile salmon (primarily chinook, *Oncorhynchus tschawytscha*, chum, *O. keta*, and coho, *O. kisutch*) were consistently higher (Goodman and Vroom 1972) at stations further "upriver" near basket Station C4 where the largest amphipod biomasses were recorded. The plankton net sampling yielded very few amphipods even at locations where the basket samplers attracted large numbers. These data suggest that only a small proportion of the amphipod population leaves cover on each high tide, and direct observations with SCUBA support this inference. The basket samplers, however, are a cumulative sampling device because they are in place for a number of high tide periods.

Anisogammarus pugettensis has been suggested as a ration item for salmon being reared in aquacultural experiments (Chang and Parsons 1975). If the basket samplers attracted this or other suitable amphipods, the technique could provide ample amphipods for initiation of mass cultures. At the locations where amphipods were most abundant at Squamish (stations C3, C4, and C5) the mean yield of amphipods was 88 mg g^{-1} *Fucus* (Table 1), equivalent to 28 g dry wt $basket^{-1}$.

Anisogammarus confervicolus apparently utilizes cover material as shelter to avoid desiccation at low tide. There is no evidence that *Fucus* is a food source for the amphipod, but microbenthic algae (e.g. *Navicula* sp., *Pylaiella* sp.) are cover material that may also be significant as food sources (Levings 1973). Nassichuk (1975) reported that another amphipod, *Hyale plumulosa*, was associated with *Fucus* in natural communities, and suggested that the presence of *H. plumulosa* might have been related to organic exudates from the alga. Since *A. confervicolus* is very catholic in its choice of substrate and cover, materials other than *Fucus*, crushed rock, and PVC ribbons would probably attract amphipods into the basket traps. Observations when habitats are exposed at low tide revealed a positive correlation between the amount of cover and amphipod biomass (Levings 1976). Smaller baskets would therefore be feasible but would attract fewer amphipods.

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Diel Movement of Walleye, *Stizostedion vitreum vitreum*, in West Blue Lake, Manitoba, as Determined by Ultrasonic Tracking

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KELSO, J. R. M. 1976. Diel movement of walleye, *Stizostedion vitreum vitreum*, in West Blue Lake, Manitoba, as determined by ultrasonic tracking. J. Fish. Res. Board Can. 33: 2070–2072.

Eight walleye (*Stizostedion vitreum vitreum*) between 2 and 5 yr of age were equipped with ultrasonic transmitters, released, and followed for periods up to 24 h. During the study period, September 24–October 2, 1975, West Blue Lake was thermally stratified. Movement was limited to the homothermous epilimnion, above 10 m, and to the region of steeply sloping bottom of about 5–10 m which was usually within 100 m of shore. Midbasin crossings of the lake were infrequent. Transmitter attachment caused temporary high activity after which a more normal rhythm was apparent with peaks of activity at dusk and dawn. The majority, 86%, of observed swimming speeds were under 1 body length s^{-1}. Since much localized activity, too restricted to measure, was apparent, these observations must be regarded as only approximations of natural activity.

KELSO, J. R. M. 1976. Diel movement of walleye, *Stizostedion vitreum vitreum*, in West Blue Lake, Manitoba, as determined by ultrasonic tracking. J. Fish. Res. Board Can. 33: 2070–2072.

Huit dorés jaunes (*Stizostedion vitreum vitreum*) âgés de 2 à 5 a. ont été équipés de transmetteurs ultrasoniques, relâchés et suivis durant des périodes allant jusqu'à 24 h. Durant la période d'étude, soit du 24 septembre au 2 octobre 1975, une stratification thermique était présente dans le lac Bleu-Ouest. Les déplacements se limitèrent à l'épilimnion homothermique, au-dessus de 10 m, soit à la région où le fond est en pente raide à environ 5–10 m, ordinairement à moins de 100 m du rivage. Il n'y eut que de rares traversées du lac par le milieu du bassin. Il y eut forte activité temporaire après la pose du transmetteur, suivie d'un rythme plus normal, avec pics d'activité au crépuscule et à l'aurore. La majorité, 86%, des vitesses de nage observées étaient inférieures à 1 longueur de corps s^{-1}. Comme il y avait beaucoup d'activités localisées, trop restreintes pour être mesurées, on doit considérer ces observations comme approximations seulement de l'activité naturelle.

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WEST Blue Lake, essentially unaffected by man, has been the site for research examining ecosystem components and factors determining productivity of the major components (Ward and Robinson 1974). Only yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*), of the seven fish species present in the lake, are abundant. Although the percid community has been under study since 1966 only indirect evidence — gillnet catches, echogram interpretation, and stomach analysis — has been available from which diel behavior could be interpreted.

This note describes diel movement of walleye during late-summer stratification using fish fitted with temperature-sensing ultrasonic transmitters.

Materials and methods — Fish were captured between September 24 and October 2, 1975, in gillnets of mesh sizes between 5.2 and 10.2 cm stretched measure. Nets were set after dark each night and continuously patrolled. Captures chosen for transmitter attachment were gently removed, placed in a perforated live box anchored approximately 7 m from shore, and held until morning. Walleye were between 2+ and 5+ yr of age and ranged in fork length from 327 to 416 mm.

Temperature-sensing ultrasonic transmitters (Bayshore Systems Corporation, Springfield, Virginia) of three different frequencies (64, 71, and 82 kHz) were used. For signal monitoring, a Bayshore Systems Corporation model RT-22 pulse rate to temperature converter/decoder was used in conjunction with a Smith Root tuneable receiver. Pulse rate was decoded and recorded as millivolts on a strip chart. Specifications and performance of transmitters and decoder are available elsewhere (Kelso 1976).

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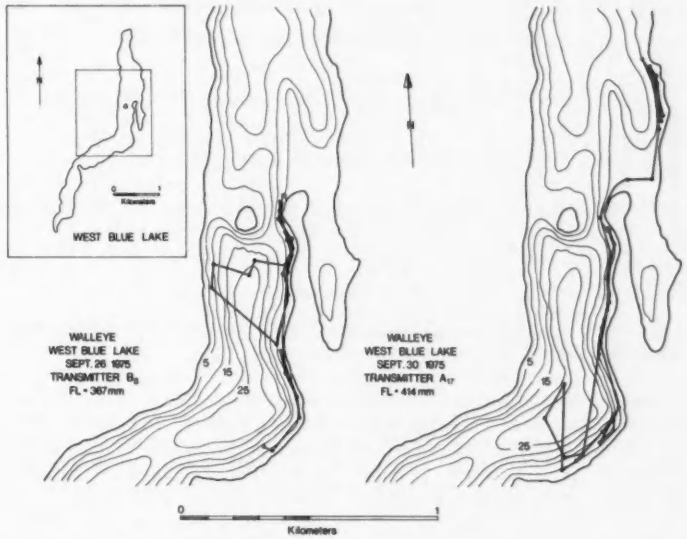

FIG. 1. Tracks of two walleye (*Stizostedion vitreum vitreum*) released in West Blue Lake, September 1975. Point of release is indicated by R.

Transmitters were sewn onto walleye just anterior to the spined dorsal fin. No anesthetic was used and attachment in this manner appeared not to adversely affect stability or movement. Effect of transmitter attachment in this manner has been partially examined (Kelso 1976). After transmitter attachment, fish were retained in aerated lake water for 15 min, then gently released.

Fish were continuously tracked from a 5-m boat with an outboard motor by maintaining the boat within 75 m of the fish and following the direction of travel. All changes in direction were noted and the location of the point of direction change was referenced to either installed shore markers or prominent shore features.

Results — Between September 24 and October 2, 1975, West Blue Lake remained stratified in all three basins. Water shallower than 10 m was essentially homothermous, generally between 10.7 and 14.7 C. Below the thermocline (10–15 m), temperatures ranged from 7.0 to 3.7 C.

Movement of walleye described herein results from tracking six fish carrying transmitters for between 14 and 24 h, and two fish for between 6 and 8 h. At all times fish remained above the thermocline in the uppermost, homothermous, 10 m of water. Temperatures obtained from transmitters were stable and consistently in the range of 10.6–11.2 C. The narrow range of temperature experienced precluded further data treatment. No excursions into colder waters were seen for any of the eight fish followed. Consequently, depths between 1 and 10 m were consistently chosen by transmitter-equipped walleye. Furthermore, these walleye generally moved along shore and were not confined to any one basin (Fig. 1). Fish rarely crossed in midbasin and stayed mostly within 100 m of shore. From temperature data, measuring depths at position fixes, and visual observation, apparently walleye primarily chose depths between 5 and 10 m.

Walleye were followed for varying periods which, when combined, extended over a 24-h period. Data from the six longer tracks was subdivided into 0.5-h intervals and combined (Fig. 2) to examine diel changes in activity (swimming speed in body lengths per second [BL/s]). Immediately following release, a period of continuous movement occurred followed by a midday decrease in activity. After sunset, activity increased rapidly, primarily short rapid bursts of speed, and then dropped off to low levels during the night. Just prior to dawn, another period of increased activity was apparent. Disregarding the period of increased swimming speed immediately following release, a pronounced crepuscular rhythm appears which includes limited activity during the day and night. Average swimming speed for all observations in the 24-h period was 0.24 BL/s.

Distances and times between position fixes were used to estimate swimming speeds of walleye. Generally, swimming speed was between 0.0 and 3.67 BL/s. The majority of observations, 86%, were under 1 BL/s. The few observations

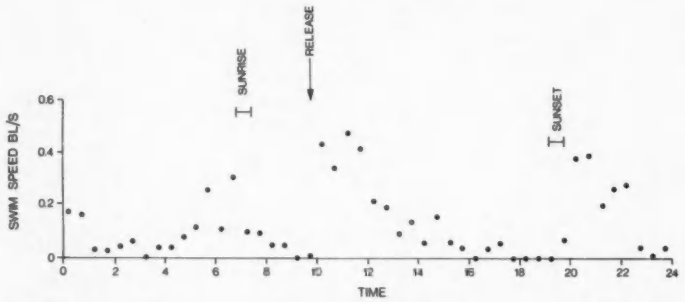

FIG. 2. Diel change in swimming speed calculated for 0.5-h periods using data from all tracks.

greater than 2 BL/s occurred just after dusk when rapid changes in position occurred. The period of activity following release was not due to short bursts of speed but was rather a period of continued movement (reorientation?) lasting up to 2 h.

Discussion — Ultrasonic transmitters caused short-term (up to 65 min) alterations in behavior (Fig. 2) and although likely resulting in other less readily detected effects, this procedure appears valid over periods used in this study (see Kelso 1976). Nevertheless, telemetry demonstrated that walleye undergo diel changes in activity with maxima after dusk and before dawn caused by bursts of swimming activity. At other times, activity appears to be at a low level, although continuous. These findings generally agree with indirect evidence provided by gillnet catches (Carlander and Cleary 1949; Lawler 1969) which tended to be more effective at night and less during the day. In West Blue Lake, catches of walleye during the day were rare and since a moderate level of activity exists (Fig. 2) visual net detection probably plays a significant role in decreased daytime catch rates.

At all time walleye were in the well-mixed epilimnion. The speculation that walleye underwent diel changes in temperature (Kelso 1972), although suggested from echograms (J. R. M. Kelso and F. J. Ward unpublished data), is apparently unfounded. During this study temperatures between 5.1 and 14.7 C were available yet walleye chose temperatures between 10.6 and 11.2 C. Summer stratification was in the process of breaking down at this time but the thermocline was still pronounced and limited the lower depth, 10 m, of walleye travel.

Acknowledgments — W. H. Hyatt spent many long hours with me in the field. Manitoba Department of Mines, Resources and Environmental Management kindly let us use Singoosh Lake cabin during our work at West Blue Lake. Drs C. K. Minns and A. B. Stasko provided helpful criticism of the manuscript.

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Metabolism of Single and Combined Doses of ^{14}C-Aldrin and ^{3}H-*p,p'*-DDT by Atlantic Salmon (*Salmo salar*) Fry[1]

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ADDISON, R. F., M. E. ZINCK, AND J. R. LEAHY. 1976. Metabolism of single and combined doses of ^{14}C-aldrin and ^{3}H-*p,p'*-DDT by Atlantic salmon (*Salmo salar*) fry. J. Fish. Res. Board Can. 33: 2073–2076.

Atlantic salmon (*Salmo salar*) fry were injected intramuscularly with ^{3}H-*p,p'*-DDT and ^{14}C-aldrin either alone or as a mixture at concentrations similar to those found in "naturally" contaminated fish; their rates of metabolism and clearance were then compared. ^{3}H-*p,p'*-DDT was cleared slowly from the fish: approximately 60% of the injected material remained 8 wk after injection. ^{14}C-aldrin was cleared much more rapidly, only 55% of the injected material remaining in the fish 1 day after injection and less than 10% remaining at the end of the experiment. ^{3}H-*p,p'*-DDT was dehydrochlorinated to *p,p'*-DDE; assuming an exponential rate of conversion, its half-life was 60 days. In contrast, 50% of the aldrin residues in the fish were epoxidized to dieldrin within 2 days. No interactions between the insecticides were observed, although aldrin apparently induced a slight increase in the fraction of total body weight accounted for by liver.

ADDISON, R. F., M. E. ZINCK, AND J. R. LEAHY. 1976. Metabolism of single and combined doses of ^{14}C-aldrin and ^{3}H-*p,p'*-DDT by Atlantic salmon (*Salmo salar*) fry. J. Fish. Res. Board Can. 33: 2073–2076.

Nous avons injecté par voie intramusculaire à des alevins de saumon atlantique (*Salmo salar*) du ^{3}H-*p,p'*-DDT et de la ^{14}C-aldrine soit seuls soit mélangés à des concentrations semblables à celles que l'on trouve chez les poissons contaminés « naturellement », et nous avons comparé leurs taux de métabolisme et de clairance. Le ^{3}H-*p,p'*-DDT est éliminé lentement du poisson: environ 60% du matériel injecté persiste 8 semaines après injection. La ^{14}C-aldrine est éliminée beaucoup plus rapidement, seulement 55% du matériel injecté demeurant dans le poisson 1 jour après injection et moins de 10% à la fin de l'expérience. Le ^{3}H-*p,p'*-DDT est converti par déshydrochlorination en *p,p'*-DDE; supposant un taux de conversion exponentiel, sa période est de 60 jours. Par contraste, 50% des résidus d'aldrine dans le poisson sont transformés par époxydation en dieldrine en dedans de 2 jours. Nous n'avons pas observé d'interactions entre les insecticides, bien que l'aldrine semble provoquer une légère augmentation dans la fraction du poids corporel total dont le foie est responsable.

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THE initial steps in the degradation by fish of *p,p'*-DDT and aldrin are, respectively, dehydrochlorination to *p,p'*-DDE and epoxidation to dieldrin. Dehydrochlorination of *p,p'*-DDT is fairly slow: assuming an exponential process, *p,p'*-DDT has a half-life of several months or longer (Zinck and Addison 1975). Aldrin epoxidation, on the other hand, is relatively rapid, with appreciable conversion taking place within a few hours (Ludke et al. 1972; Wells et al. 1973). Rates of the two processes cannot be compared directly from these data since the experiments were carried out in different species of fish under varying conditions. In this note, we describe the direct comparison of rates of the two processes occurring simultaneously in the same group of fish. Since both *p,p'*-DDT and aldrin and their principal metabolites induce the microsomal enzymes which in other organisms catalyze degradation of various foreign compounds (Capdevilla et al. 1973; Den Tonkelaar and Van Esch 1974), their possible interaction was also examined.

Materials and methods — ^{3}H-ring-labeled *p,p'*-DDT was bought from New England Nuclear, Inc. and aldrin labeled with ^{14}C was bought from Amersham Searls. Each was diluted with unlabeled material (Supelco Inc.) to final specific activities of 10.2 mCi/mM (^{3}H-*p,p'*-DDT) and 0.9 mCi/mM (^{14}C-

[1]Bedford Institute of Oceanography Contribution.

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aldrin). Both compounds contained less than 0.1% peak area as material other than the compound specified when subjected to GLC (Addison et al. 1972). Both compounds were dissolved in 95% ethanol to give solutions of 6.3 μg/μl *p,p'*-DDT or 7.5 μg/μl aldrin. A mixture containing 4.9 μg/μl *p,p'*-DDT and 6.6 μg/μl aldrin was also prepared.

Atlantic salmon (*Salmo salar*) weighing from 5 to 10 g were taken at random from the laboratory's stock of freshwater-maintained fish and divided into four groups of 60. These included a control group not exposed to insecticide, an experimental group treated with *p,p'*-DDT and aldrin, and to allow detection of any interaction between the two insecticides, two groups treated with either *p,p'*-DDT or aldrin alone. They were kept separately in fiberglass tanks with flowing fresh water at 15 C, generally as described previously (Addison and Zinck 1975) and were offered Ewos fish chow ad lib. twice daily except on weekends.

Each fish was injected intramuscularly near the dorsal fin using a Hamilton No. 701N syringe with a) 95% ethanol (control group); b) a mixture of ^{3}H-*p,p'*-DDT and ^{14}C-aldrin; c) ^{3}H-*p,p'*-DDT; and d) ^{14}C-aldrin. Injection volumes (around 5 μl) were chosen to produce initial pesticide concentrations of 5 ppm (on a whole body basis) of each pesticide, whether alone or in combination. At intervals of 1, 14, 28, 42, and 56 days after injection, 8–10 fish were removed at random from each group. They were killed by a blow on the head, weighed, and the livers removed and weighed separately. The whole fish, including liver, was then extracted as described previously (Zinck and Addison 1975). Extracts were analyzed for *p,p'*-DDT, aldrin, and their metabolites using a combination of GLC, TLC, and single- and double-label liquid scintillation counting generally as described elsewhere (Anon. 1969; Darrow and Addison 1973; Addison and Zinck 1975).

Results and discussion — Two fish in the ethanol-injected (control) group died 14 and 23 days after injection. One fish in the ^{3}H-*p,p'*-DDT-injected group died (11 days after injection) and four died in the ^{3}H-*p,p'*-DDT and ^{14}C-aldrin group (three at 3 days and one at 14 days after injection). Analytical data for the dead fish (weight, lipid content, proportion of total weight accounted for by liver, pesticide residue burden, and percent metabolism of injected pesticides) were not significantly different from their surviving counterparts.

Control-group fish contained residues of the DDT group (*p,p'*-DDE + *p,p'*-DDD + *p,p'*-DDT) to a total of < 0.5 ppm wet wt. No residues of aldrin or dieldrin were detected in these fish.

Fish weight increased by approximately 70% (from a mean of 6.5 to 11 g) between injection and termination of the experiment 56 days later. There was no statistically significant difference ($P > 0.05$ by *t*-test) between groups at any point during the experiment. Lipid content remained fairly constant at 3.5 ± 1.0% wet wt (mean ± SD of 152 determinations) and did not differ significantly between groups sampled at the same stage of the experiment, or within groups throughout the experiment. There was a general correlation between lipid content and weight, which we have noted previously (Zinck and Addison unpublished data).

The fraction of body weight accounted for by liver was slightly but not significantly ($P > 0.05$) greater in those fish treated with ^{14}C-aldrin than in the controls or the ^{3}H-*p,p'*-DDT-treated groups up to 42 days after injection (Fig. 1). This elevation was not detectable 56 days after injection. Induction of microsomal enzyme systems in other species treated with chlorinated hydrocarbons may be accompanied by an increase in the ratio liver weight to body weight (Litterst et al. 1972) and so these results might be interpreted as indicating that some such induction had occurred in the aldrin-treated fish. Other estimates of microsomal enzyme induction were not available.

The amount of radioactive material recovered after injection decreased over the experimental period. ^{3}H-material was eliminated only slowly from the fish: by the end of the experiment, approximately 60% of the theoretical dose injected remained. ^{14}C derived from aldrin was eliminated

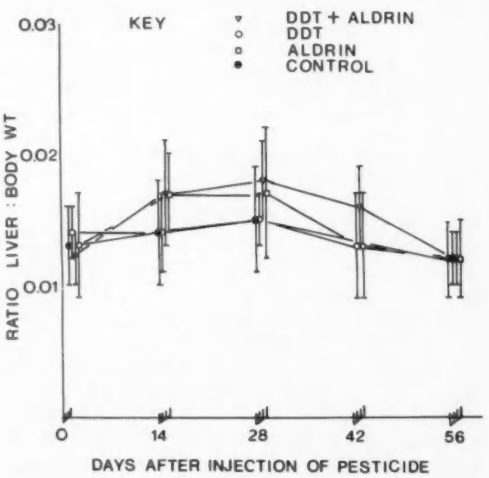

FIG. 1. Fraction of body weight accounted for by liver as a function of time after injection in Atlantic salmon (*Salmo salar*) injected with ^{3}H-*p,p'*-DDT and ^{14}C-aldrin alone or in combination (mean ± SD of 8–10 determinations).

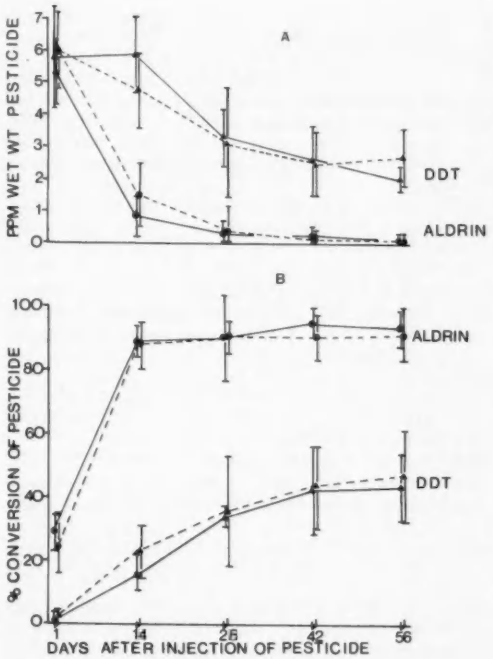

FIG. 2. A, Concentration of ^{3}H- and ^{14}C-labeled residues in salmon at times after injection of ^{3}H-*p,p'*-DDT and ^{14}C-aldrin alone (———) or in combination (– – – – –) (mean ± SD of 8–10 determinations). B, Extent of dehydrochlorination of ^{3}H-*p,p'*-DDT and epoxidation of ^{14}C-aldrin following their injection alone (———) or in combination (– – – – –) into salmon (mean ± SD of 8–10 determinations).

much more rapidly: only 55% of the theoretical injected dose remained 1 day after injection and less than 10% remained in the fish at the end of the experiment (Fig. 2A). Clearance of ^{3}H or ^{14}C from the group treated with the mixture of *p,p'*-DDT and aldrin did not differ at any stage during the experiment from those treated with either compound alone; thus, the slight degree of enzyme induction implied by the liver weight changes in the aldrin-treated groups was not reflected in a change in the rate of clearance of *p,p'*-DDT derived material.

Radioactive material remaining in the fish was in the form of either the parent compound (i.e. *p,p'*-DDT or aldrin) or one metabolite (*p,p'*-DDE or dieldrin, respectively). The rate of *p,p'*-DDE production was much faster than that which we had observed previously in trout (*Salvelinus fontinalis*) and is illustrated in Fig. 2B. A plot of fraction of ^{14}C-*p,p'*-DDT remaining unchanged vs. time was fitted best ($r = 0.97$) to an exponential equation. Assuming first order kinetics for the process *p,p'*-DDT had a half-life of approximately 60 days, compared to the 255 and 408 days calculated previously (Addison and Zinck 1975; Zinck and Addison 1975). This may reflect species differences in the capacity of *Salmo* and *Salvelinus* to handle *p,p'*-DDT, or the fact that fish used in the present work were much smaller than those used previously, and hence would have had a higher overall metabolic rate. The ability of fish to accumulate *p,p'*-DDT from water varies inversely with body weight (Murphy 1971) reflecting an inverse relation between body size and weight-specific metabolism.

Conversion of ^{14}C-aldrin to dieldrin was much more rapid than that of *p,p'*-DDT to *p,p'*-DDE (Fig. 2B). Data describing the rate of aldrin epoxidation were best fitted to a power function; for comparison with the rate of *p,p'*-DDT dehydrochlorination, the time required for expoxidation of 50% of aldrin residues in the fish was between 1 and 2 days. Two weeks after injection of ^{14}C-aldrin, over 90% of the ^{14}C material was in the form of dieldrin. Its rapid expoxidation and clearance from the fish (Fig. 2A) suggest that aldrin is excreted after conversion to dieldrin. Other studies have shown that dieldrin accumulated by fish is cleared rapidly (Gakstatter and Weiss 1967; Grzenda et al. 1972).

There was no evidence that the two insecticides administered together to the fish interacted in any way. In spite of the slight increase in liver weight noted in the ^{14}C-aldrin-treated groups, the elimination and metabolism of *p,p'*-DDT in the group treated with both *p,p'*-DDT and aldrin did not differ significantly from that in the group treated with *p,p'*-DDT alone. Similarly, injection of *p,p'*-DDT had no detectable effect on ^{14}C-aldrin clearance or epoxidation. Interactions between storage of the DDT group and cyclodienes in trout have been reported (Mayer et al. 1970), but in general those effects were noticeable only at whole body concentrations appreciably higher than those reported here. No effects of residue storage on rates of metabolism of the insecticides administered in that experiment were reported.

Concentrations of *p,p'*-DDT, aldrin, and their metabolites reached in the fish during this experiment (3–5 ppm wet wt DDT-group, 0.1–5 ppm aldrin and dieldrin) are similar to those found in "naturally" contaminated fish (Henderson et al. 1971). However, these levels were attained by a single intramuscular injection, rather than by "normal" uptake from food or across gills. The handling of organochlorines may be affected by their routes of uptake (cf. data of Henderson et al. 1959; Buhler et al. 1969). Our results should

therefore be interpreted as showing that residue burdens similar to those found in environmental samples, but acquired by a single intramuscular injection, do not interact with each other's clearance or metabolism.

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Improved Reagent Dispenser for the Determination of Dissolved Oxygen in Sea Water

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CUNNINGHAM, C. C., D. D. W. CONRAD, J. D. MOFFATT, AND E. M. LEVY. 1976. Improved reagent dispenser for the determination of dissolved oxygen in sea water. J. Fish. Res. Board Can. 33: 2076–2078.

An improved dispenser for delivering the reagents used in the quantitative determination of dissolved oxygen in sea water is described.

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Nous décrivons un distributeur amélioré de réactifs utilisés dans la détermination quantitative de l'oxygène dissous dans l'eau de mer.

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IN an earlier publication Duedall et al. (1971) described a device for dispensing the two reagents ($MnCl_2$ and NaOH-NaI) used in the Carritt and Carpenter (1966) modification of the classical Winkler method for the determination of dissolved oxygen in sea water. Their device consists of two syringes in which the pistons are manipulated by a crank-operated mechanism with one revolution of the crank resulting in sufficient linear advancement of the pistons to deliver 1 ml of reagent from each syringe. Syringes are refilled from reservoirs by appropriate placement of the three-way valves and reverse cranking. Although this device is an improvement over the use of individual pipettes (which sooner or later results in contamination of the reagents), it has a number of serious shortcomings: the pitch of the drive screw must be matched to the dimensions of the syringe being used and, therefore, careful machining is required; the horizontal placement of the syringes makes filling them without entrapping air an exceedingly onerous task while subsequent expulsion of this air is virtually impossible without tipping the device and spilling the reagents; and the three-way valve systems for dispensing the reagents and refilling the syringes proved to be a frequent source of annoyance in that they always seem to be in the wrong position resulting in either drawing the seawater sample into the dispenser tubing and destruction of the sample or admitting air to the syringes.

During the past several years, a number of commercially available reagent dispensers and several of our own design have been evaluated by our group. As a result of this experimentation there has gradually evolved what we consider to be the ideal device (Fig. 1) for dispensing oxygen reagents, while variations of this general design have proven useful for a variety of other liquid dispensing operations both in the field and in the laboratory.

The dispenser consists of two Cornwall (Becton, Dickinson & Co., Canada Ltd., Clarkson, Ontario) metal pipette holders (1) fastened in a wooden support (2) which also serves as a holder for the two 1-liter amber polyethylene reagent bottles (3). Each pipette holder contains a 3-cm³ plastic syringe (4) with a Luer-Lok tip to which is attached a Cornwall filling unit (5). This leads by way of a rubber check valve and a disposable hypodermic needle (18 gauge × 1½ in.) (6) to a length of polyethylene tubing (ID 0.047 in.) (7) through which the reagent is delivered to the seawater sample. The remaining arm of the filling unit is connected via a rubber check valve and gum rubber or tygon tubing (8) to the reagent reservoir (3). A Cornwall stainless steel sinker in the end of this tube ensures that it remains at the bottom of the reagent bottle.

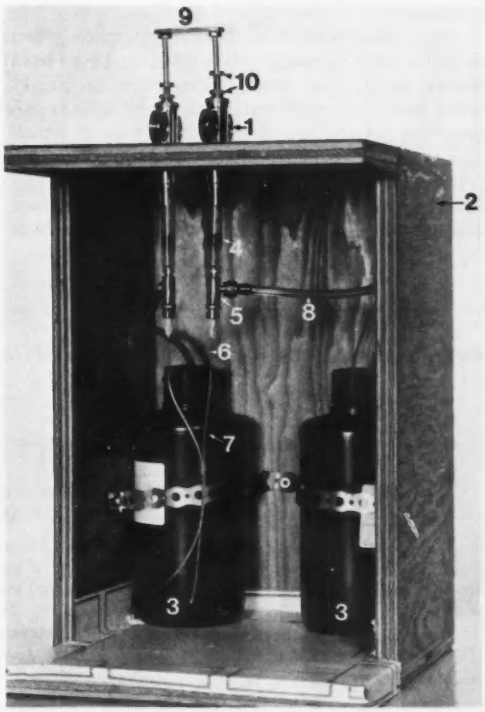

FIG. 1. Improved reagent dispenser set up for use on oceanographic cruises.

The two pipette holders are joined by a metal

yoke (9). When the stops (10) on the pipette holders are properly adjusted, a single depression of the yoke delivers 1 ml of both reagents simultaneously. On releasing the yoke, the spring mechanisms in the pipette holders automatically return the syringe pistons to their initial positions and thereby refill the syringes. Repeatability is better than 0.6% (coefficient of variation) for the 1-ml volumes required by the analytical procedure.

These dispensers have been thoroughly tested on numerous oceanographic cruises. They have proven to be free from malfunction or breakdown even under the extremes of conditions encountered at sea and despite the abuse to which equipment is sometimes subjected in the field. (However, in the event that a breakdown should occur, the difficulty should be readily diagnosed and remedied by replacing the faulty component from a kit of spare sparts.) Because of their reliability and simplicity, these dispensers have become standard equipment on all cruises from the Bedford Institute of Oceanography in which oxygen analyses are to be carried out. Their reputation is well deserved.

Oh! yes, they have one further highly desirable feature — their low cost — less than $75 for both components and labor.

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Seasonal Growth Rates of Mooneye (*Hiodon tergisus*) from the Assiniboine River

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GLENN, C. L. 1976. Seasonal growth rates of mooneye (*Hiodon tergisus*) from the Assiniboine River. J. Fish. Res. Board Can. 33: 2078–2082.

Length increments, calculated from fish measured at capture and from estimates of back-calculated lengths at time of formation of the most peripheral scale annulus, were used to determine the growing season and seasonal growth rates of mooneye (*Hiodon tergisus*). Data from 670 fish indicate that mooneye grow rapidly from June to mid-August with little or no growth occurring during other months. Length increased as a linear function during summer. Summer growth rates of 0.89, 0.58, 0.49, 0.44, 0.23, and 0.16 mm/day were estimated for fish aged I–VI, respectively.

GLENN, C. L. 1976. Seasonal growth rates of mooneye (*Hiodon tergisus*) from the Assiniboine River. J. Fish. Res. Board Can. 33: 2078–2082.

Nous avons déterminé la saison et les rythmes saisonniers de croissance de la laquaiche argentée (*Hiodon tergisus*) en nous fondant sur les augmentations de longueur calculées à partir de mesures effectuées au moment de la capture et de rétrocalculs de la longueur au moment de formation de l'annulus le plus rapproché de la périphérie de l'écaille. Les données recueillies sur 670 poissons indiquent que la laquaiche argentée croît rapidement entre juin et la mi-août et que la croissance est faible ou nulle durant les autres mois. La longueur augmente suivant une fonction linéaire en été. Des taux de croissance estivale de 0.89, 0.58, 0.49, 0.44, 0.23 et 0.16 mm/jour ont été estimés chez des poissons d'âges I–VI respectivement.

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PREVIOUS studies of growth in mooneye, *Hiodon tergisus*, have determined annual growth rates or fish size at different ages. Johnson (1951) reported length and weight of mooneye aged I–VIII captured from Lake Erie and Lake St. Clair. Van Oosten (1961) and Glenn (1975a) presented annual growth increments of consecutive year-classes of mooneye based on data from back calculations of body-scale measurements but they did not indicate growth rates during the year or length of growing season. The purpose of

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this investigation was to determine the main growing season of mooneye in the Assiniboine River and to calculate growth rate in length of fish aged I yr and older throughout the year.

Materials and methods — As this study represents further analysis of data published (Glenn 1975a) for annual growth rates, detailed methods of specimen sampling, aging of mooneye, and the back calculation of length at time of annulus formation can be obtained from the earlier publication. Basically, these methods involved netting mooneye in the Assiniboine River at approximately 2-wk intervals between November 17, 1972 and November 2, 1973. Total body length of each mooneye was measured and several body scales were removed for examination with a microprojector. Data from the magnified scale image were used to obtain fish age, back-calculated body lengths at respective annuli, and time of annulus development during 1973. Counting the number of scale annuli provided an estimate of fish age. Distances along scale radius between each annulus and scale focus plus the total scale radius were measured. These scale measurements and the observed total body lengths were then applied to the body length to scale length ratio with a correction factor, as described by Fraser (1920), to obtain an estimate of the back-calculated length at each annulus. Glenn (1975a) established a correction factor of 53 mm for the ratio and determined the beginning of the growing season (time new annulus developed at scale periphery) to be the 1st wk of June for the mooneye examined.

To obtain an estimate of growth rates of respective age-groups of mooneye, every fish collected at each sample period was aged and its growth increment determined. Growth increment was calculated as the difference between observed body length and the back-calculated body length at the peripheral scale annulus. Thus, the increment was an estimate of growth between 1st wk of June and time of capture. When several mooneye of the same year-class were netted at a given sample period, the mean increment was computed. Data from age groups VI–IX were combined because few samples of those older fish were collected at each netting period.

Least square regression lines were fitted to increments of each age-group over time periods to provide estimates of growth during the year. Data collected between November 17, 1972 and May 28, 1973 were separated from data recorded from June 12 to November 2, 1973 because they represented increments of two year-classes of the same age.

Results and discussion — Determination of the growing season and estimates of seasonal growth in length for mooneye aged I and older were calculated from measurement of 670 fish sampled from the Assiniboine River during 1972–1973. Data from these samples indicate, in general, a season of rapid growth which extended between the 1st wk of June and mid-August (Fig. 1). Following the main growing season, increase in fish

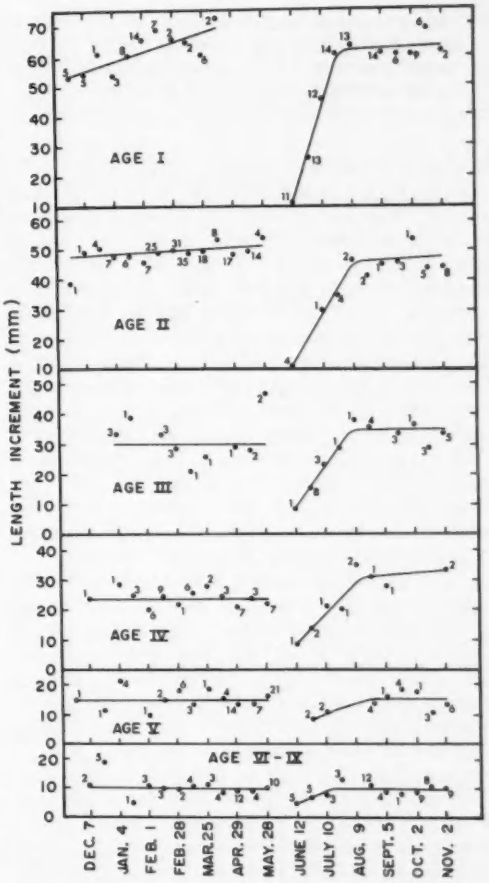

FIG. 1. Seasonal rate of growth in length for mooneye (*Hiodon tergisus*) older than age I captured between November 17, 1972 and November 2, 1973. The mean increment is an estimate of growth between time of capture and previous June (annulus is formed in early June and a year-class was assigned to the next age-group at that time).

length is limited or negligible. The main growing season may even be shorter for mooneye aged I because the mean increment calculated for July 25 was similar to those determined for sample periods between August and November.

There may be some growth during winter for the younger age-groups of mooneye. Slopes of linear least square regression lines fitted to increments recorded for fish captured between November 17, 1972 and May 28, 1973 provided estimates of total length gains of approximately 20, 7, and 3 mm for age-groups I–III, respectively. However, slopes of lines calculated from data for

TABLE 1. Mean length increments of 176 mooneye (*Hiodon tergisus*) captured from the Assiniboine River during the summer and autumn of 1973. *N* represents number of specimens captured, L_t is mean total body length at time of capture, L_j is mean back-calculated lengths of *N* specimens, and G is growth increment (millimeters) between 1st wk of June and capture date.

	Sampling dates							
Parameter	June 12	June 27	July 10	July 25	Aug. 9	Aug. 23	Sept. 5	Sept. 19
				Age-class I				
N	11	13	12	14	13	—	14	6
L_t	131	146	158	171	178	—	171	172
L_j	119	120	112	110	115	—	110	111
G	12	26	46	61	63	—	61	61
				Age-class II				
N	4	—	1	4	2	2	1	3
L_t	186	—	230	194	232	230	220	227
L_j	175	—	200	159	185	188	175	181
G	11	—	30	35	47	42	45	46
				Age-class III				
N	1	8	3	1	1	4	—	3
L_t	220	230	258	230	275	253	—	255
L_j	211	214	235	201	237	217	—	222
G	9	16	23	29	38	36	—	33
				Age-class IV				
N	1	2	1	1	2	1	1	—
L_t	235	285	285	287	275	270	280	—
L_j	227	271	263	266	240	238	252	—
G	8	14	22	21	35	32	28	—
				Age-class V				
N	—	2	2	—	—	4	1	4
L_t	—	282	290	—	—	280	280	276
L_j	—	274	279	—	—	266	264	260
G	—	8	11	—	—	14	16	16
				Age-class VI+				
N	5	5	3	3	—	12	4	1
L_t	315	303	301	306	—	294	286	295
L_j	310	296	294	293	—	283	277	287
G	5	7	7	13	—	11	9	8

age-groups IV, V, and VI–IX were negative or approached zero and signify that older mooneye may experience little or no increase in length between late autumn and the following spring. The occurrence of negative slopes was attributed to small sample sizes of the older age-groups. Increments computed for fish netted between August 23 and November 2 would also indicate limited growth by all year-classes during autumn of 1973.

The short 2.5-mo growing season is similar to the duration of growing seasons of other temperate-zone fish species. Smith and Pycha (1960) recorded that greater than 90% of the annual growth was completed by August for young walleye (*Stizostedion vitreum vitreum*) and Gerking (1966) found approximately 90% of the total-length increment completed in sunfish by September. Kennedy and Sprules (1967) observed steady growth during June and July for goldeye (*Hiodon alosoides*). They also state that growth is slow during autumn and that "very little growth, if any, occurs between October and the following June."

The purpose of this study was to estimate seasonal growth rates of mooneye rather than to discuss growth models. Therefore, the detailed methods and results of "curve fitting" for curvilinear regressions will not be presented. When least squares curves were fitted to the increment of each fish in each age-group for sample periods June 12–August 9, it was found that the summer

growth in length during 1973 was best expressed as a linear function for fish aged II–VI. A hyperbolic function was the best fit ($r = 0.87$) for age-group I followed by the linear regression ($r = 0.86$). It is probable that mooneye growth during summer did follow some type of sigmoid growth curve but that the sampling procedure did not supply sufficient data. The absence of data for early June and the few increments during the interval July 25–August 23 are most critical for the calculation of the "acceleration phases" of the logistic curve. The linear results obtained may represent only the logarithmic phase of the sigmoid curve. The hyperbolic function computed for mooneye aged I may have resulted from differences in growing season. If young mooneye have a shorter growing season and if the growth increments from sample period August 9 are not used for the calculation of the equation, the best fit for this age-group was a linear function.

Slopes of the linear equation were: 0.89, 0.58, 0.49, 0.44, 0.23, and 0.16 for age-groups I–VI, respectively. The slope, which is an estimate of mean daily increase in millimeters between June 12 and August 9, indicates that length increments progressively decrease with each age-group. Similar trends of length change can be noted from the mean increments calculated for each age-group for any single sampling period (Table 1).

On the assumption that there is little growth in winter, the mean length increments obtained from samples netted between August and November would indicate that growth during 1973 was average. This conclusion is based on comparison of the autumn increments with annual length increments calculated by Glenn (1975a).

Estimates of seasonal growth rates in fish populations can be obtained from a direct procedure which uses changes in sizes of fish captured during the year and from an indirect method involving changes in sizes between time of annulus formation and time of capture. The direct method would have been ideal if 1) it were possible to obtain the size change of all the same samples during the time interval, or 2) the mean sizes of different groups of samples were constant at any sampling date. Use of the direct procedure was not possible in the present study because different specimens were examined at each sampling date and because the back-calculated lengths at annulus formation indicate that lengths of specimens varied during the 1st wk of June. Furthermore, when seasonal growth data were applied to the direct procedure, the effects of net selectivity were believed to seriously mask true growth estimates. For example, the actual observed mean lengths at time of capture for fish aged V were greater in June and July than mean lengths of specimens captured in late August or September (Table 1). The growth increments, however, progressively increased during the summer.

I believe that the indirect method provided a reliable estimate. The procedure permitted estimation of growth from data on fish with different growth histories. A mooneye could be larger or smaller than the year-class norm at time of capture and annulus formation and still have a length increment similar to those of its age cohorts. Influence of net selectivity should be minimal because length at annulus formation and time of capture, hence growth increment, were obtained from the same sample. Growth data presented may, however, be biased. Effects of small sample sizes, differences in time of annulus formation between fish, differential growth rate between sexes, exploitation, and growth compensation have not been established.

Conditions responsible for the rapid increase in length of mooneye during the period June to mid-August are not known. I believe, as Paloheimo and Dickie (1966) have suggested, that fish metabolism and growth are affected by environmental and physiological factors. Smith and Pycha (1960) noted positive correlations between water temperature and walleye growth. Gerking (1966) found no correlation between growth and water chemistry such as dissolved oxygen, carbonates, or sulphate content in bluegill (*Lepomis macrochirus*). Gross et al. (1965) presented evidence that growth was related to light and food consumption in green sunfish (*L. cyanellus*). Growth in mooneye does not seem entirely dependent on type of diet or on seasonal feeding patterns. Glenn (1975b) noted that all age-groups of mooneye fed on insects throughout the year. He also noted that, in general, the amount of food in stomachs examined was greater during spring and autumn and not during June and July when rapid growth occurred. However, the digestive rate may be rapid during summer and this may account for the reduced amount of food in the stomachs of the mooneye he analyzed. Further investigations into physiological and environmental effects on growth are required.

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PERSPECTIVES

Analysis of Large-Scale Ecological Systems[1,2]

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Contents

2084 ABSTRACT/RÉSUMÉ
2084 INTRODUCTION
2084 SYSTEMS ANALYSIS IN ECOLOGY
2085 SCALE-DEPENDENT PROCESSES
2086 INFORMATION MODEL
2088 DISCUSSION
2088 ACKNOWLEDGMENTS
2088 REFERENCES

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Abstract

KERR, S. R., AND M. W. NEAL. 1976. Analysis of large-scale ecological systems. J. Fish. Res. Board Can. 33: 2083–2089.

Large spatial and temporal scales imply a proportional need for large volumes of data. Ecological systems exhibit different patterns of variability as a function of scale. It follows that large-scale ecological systems are appropriately observed at a number of different spatial and temporal scales, further complicating the data requirements for various kinds of analysis. The concept of an "information model," in conjunction with an effective data base management system, enables an analytical approach to large-scale ecological systems that is relatively unconstrained by preconceived organizational structures in the data base.

Résumé

KERR, S. R., AND M. W. NEAL. 1976. Analysis of large-scale ecological systems. J. Fish. Res. Board Can. 33: 2083–2089.

A de grandes échelles dans l'espace et dans le temps correspond un besoin proportionnel de grands volumes de données. La variabilité des systèmes écologiques diffère dans ses modalités en fonction de l'échelle de grandeur. Les systèmes écologiques à grande échelle doivent donc être observés à plusieurs échelles différentes dans l'espace et dans le temps, ce qui complique davantage les besoins en données pour diverses sortes d'analyses. Le concept d'un « modèle informatique », couplé à un système efficace de gestion d'un fichier central, permet une approche analytique aux systèmes écologiques à grande échelle, approche relativement libre de structures organisationnelles préconçues dans le fichier central.

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Introduction

Analysis of large ecological systems often involves special problems. In part, difficulties can arise because of the larger volumes of data needed to maintain sampling resolution as the scale of the system is increased in space or in time. Large data files are difficult and expensive to collect, verify, access, and analyze. A frequent result is that an investigator must use data that were initially collected for some other purpose, and the consequent problems of file verification and manipulation must be resolved before the required information can be extracted in usable form.

But just as Lake Superior is something more than Linsley Pond "writ large," large systems may incorporate ecological processes that are not evident in smaller systems. Scale-dependent processes therefore tend to compound the data requirements and the analytical complexities associated with large systems.

For these reasons, analysis of large-scale ecological systems is often, but not necessarily, data intensive. For some ecological problems, appropriate analytical simplifications exist which obviate the need for large data files. Ecological theory is not richly provided with such simplifications, however, and data-intensive analysis is likely to be needed for a wide range of large-scale problems in the foreseeable future. In what follows, we outline a useful approach to the data-intensive aspects of large-scale ecological analysis.

Systems Analysis in Ecology

A priori, we explain our use of basic terms. The notion of "system", as in the term "ecosystem", has been used for some time in ecology. In some sense, the idea is probably accepted and used by most ecologists. The derivative term "systems analysis" is apparently restricted, by some ecologists, to the analysis of reductionist models, excluding the use of integral system models (Kerr 1976). To avoid confusion with this peculiarly narrow definition, we adopt here Ashby's general definition of a "system" as nothing more than a list of variables (Ashby 1956). As ecologists, we are interested in variables that are reliably observable in identifiable, scientifically interesting portions of the biosphere, and that, taken together, exhibit some kind of integrated, emergent behavior. Analysis of such lists of variables, by whatever means, is what we understand to constitute "systems analysis" in ecology. Despite its ambiguities, this broad definition is in keeping with the sense of general systems theory (Klir 1972), and serves to convey our usage in what follows.

As any field ecologist knows very well that the

number of variables potentially observable in any portion of the biosphere is large, it follows that the initial challenge is to reduce the essentially unlimited list of candidate observables to manageable proportions. In consequence, there will be inevitable differences between the "real" system, with its enormous number of potential observables, and any given system representation that we construct for analytical purposes. The challenge is to reduce the list of variables without compromising the adequacy of the resulting system representation, or model, that we use to investigate a given problem. If we fail in this, there is serious risk of confusing the behavior of misleading models with the behaviors of the real entities which they purport to mimic (Kerr 1974a).

Our aim, therefore, is to select the minimum list of variables that is necessary to account for the ecological behaviors that are of interest. Our selection of variables is entirely dictated by the conceptual outlook, or paradigm (Kuhn 1970), that we bring to the problem. In practice, the paradigm constraint is particularly serious with large-scale ecological systems, because of the substantial practical difficulties that hinder observation of variables over an adequate time series or spatial scale. Conceptual outlooks can change, and data collected under the influence of one paradigm may or may not be suitable for investigations addressed to another. Apart from the purely economic considerations inherent in repeating an unsuitable sampling regime that is large in spatial terms, time-series data that are unsuited to an analysis, by virtue of having been collected under a different paradigm, may sometimes be irreplaceable. In ecology it seems generally true that if the appropriate variables have not been measured, then a great deal of time and effort has been lost.

An example may clarify this relatively abstract point. There is considerable current interest in devising measures for evaluating the sensitivity of ecological systems to exogenous stress. Numerous methods have been proposed, most of which are variously based upon the typological (species-oriented) paradigm that has dominated post-Linnaean biology. One alternative approach that seems promising is quite independent of the typological paradigm; it is based on ecological size structure. Sheldon et al. (1972) noted that concentrations of particulate matter in marine pelagic ecosystems are relatively uniform when grouped in logarithmic intervals of particle size. It is a matter of simple algebraic manipulation to show that this is a reasonable result, quite in keeping with theoretical expectation. Predictable size structures could emerge quite commonly in natural systems (Kerr 1974b). Woodwell (1970) noted the dynamic side of this phenomenon in his observation that ecological communities generally show a diminished mean size in response to impressed stress. Taken together, this work suggests that analysis of community size structure could yield useful information concerning the "stability" and stress tolerance of natural systems (Kerr 1974b). Unfortunately, appropriate data to further evaluate this hypothesis are not readily available because the prevailing ecological paradigm is based upon typology not size structure. Surprisingly, it is not feasible, for example, to extract a mean-size statistic from the lengthy time series of fishery production data from the Laurentian Great Lakes. The accepted paradigm that governed the historical collection of these data does not permit such analysis. The implication is that we might save a great deal of time, effort, and money, and miss fewer analytical opportunities, if our data acquisition could be made as independent as possible of the paradigms that prevail at the time of data collection. Before considering means for accumulating paradigm-independent data files, some further complications associated with large-scale systems should first be considered.

Scale-Dependent Processes

Nothing within the purview of systems theory suggests that large-scale systems are necessarily unique in any fundamental way, but some significant distinctions must nevertheless be faced by the analyst. There is an array of further complications to be dealt with, in the sense that new sources of variability emerge as the spatial or temporal scales of a system are expanded.

Investigation of scale-dependent phenomena is yet in its infancy in ecology, although some substantial observations point to its reality (Platt 1972a; Platt et al. 1970; Sutcliffe et al. 1971). In essence, this and related work shows that the variance patterns associated with ecological measurements taken in marine ecosystems exhibit important regularities that are associated with the spatial scales of physical processes occurring in these environments (Platt and Denman 1975). Thus, Platt (1972a) has shown that the variance of phytoplankton concentrations measured, under certain simplifying conditions, over scale factors of approximately 10s–100s of meters, exhibits a distribution characteristic of the Kolmogorov decay function for turbulent processes. The implication from this and similar work is that ecological processes are entrained to the inherent

scales of the physical environment in which they occur. Morowitz (1974) has recently provided a global, evolutionary context for this view.

Therefore, the pattern exhibited by variables measured at say, the centimeter scale of observation can be qualitatively different from similar measurements based on a kilometer scale. This follows, not simply because a larger sampling effort is required to secure representative data from a larger area, but because ecological measurements taken at the level of microturbulent processes do not exhibit the same pattern at the scale of Langmuir or similar convective processes nor at the larger scale of thermal bars or major current structures.

Similar considerations apply to changes in temporal scale. Indeed, a major ecological problem is to couple time-variant processes with inhomogeneities that occur in space. Platt (1972a) using spectral analysis has successfully achieved analytical transposition from the temporal to spatial domains, nicely illustrating this parallelism.

Although physical and chemical processes are doubtless ultimately responsible for the scale-dependent variabilities exhibited by ecological systems, the relationship is not necessarily direct. Thus, Lawrie and Rahrer (1972) found that the utility of the historical data from the lake trout (*Salvelinus namaycush*) fishery of Lake Superior is seriously compromised because it does not correspond to the natural scale of the discrete lake trout stocks. Sampling districts were inappropriately scaled, masking the dynamics of the individual stocks. In this instance, the scale-dependent factor was population distribution, which is indirectly affected by abiotic environmental structure.

Accordingly, there is reason to believe that large-scale ecological analyses differ in some operational senses from small systems, and that these differences must be accounted for in our analytical procedures. In particular, we conclude that analysis of large-scale systems must encompass the effects of patterns of variability that are not expressed in smaller systems. This conclusion appears secure at least until such time as we possess, in Platt's (1972b) terms, "a general theory of variability in relation to biological production systems." In the absence of such a theory, there is no general procedure for simplifying the effects of ecological scale.

In short, we conclude that large-scale ecological analysis is necessarily likely to remain data intensive, for a variety of reasons. Because voluminous data files are expensive to collect and maintain and can easily constitute monuments to missed analytical opportunity, considerable care should preface compilation of any large-scale data series. In particular, the data should be organized in some manageable way that is not sensitive to the ecological paradigms that are prevalent at the time the collection is initiated. Data-management protocols that are utilized should recognize the likelihood of different needs for information extraction, at the behest of new paradigms. It remains to describe some effective means to achieve these ideals.

Information Model

A general approach to these goals is to interpose what we call an "information model" between the real ecological entity and the models and analytical procedures that are thought to be applicable at a given time. As such, the information model consists of a collection of "primary variables" that describe the structure of the system, through its several hierarchical levels of ecological organization, in time and space. The definition of primary variables, observables that cannot be simply derived from other variables measured at the same or a lower hierarchical level, is necessarily going to change with time, with enhanced understanding of the system, and with development of more sophisticated technology for measuring. Therefore, the information model itself will be a dynamic product of an iterative feedback from the analysis process: it will never be independent of analytical paradigms, but always approaching that state.

In effect, we are defining the information model as an ecosystem data base, which is constructed according to different principles than have traditionally been applied to data base design. Data base design conventionally works back from rigid definitions of the desired outputs as a means of determining the required input data. But if we follow conventional practice and design a data base according to a set of preconceived outputs or results, we are risking the danger of restricting the set of potential system behaviors to those that impinge directly on the specific goals or ideas we have in mind at a given time. At best, the resulting data base is restricted to investigation within a specific paradigm or set of paradigms. Because of the cost and difficulties inherent in data collection from large-scale ecological systems, the approach we endorse is precisely the reverse of conventional practice.

In our view, every effort should be made instead to provide the most general representation of the real ecological entity in the information model that we construct, and to avoid defining the system's purpose according to current ideas.

Information system design should, therefore, emphasize the input side of the analysis, with a view to establishing as generalized a basis as possible, to support a wide variety of analytical procedures. This point of view is not unique with us. The output-oriented tradition in business systems design has begun to change in favor of an input-oriented approach that focuses on the development of a prototype system, which in turn becomes an adequate representation through sustained interaction with the users of the system (Appleton 1973).

An information model, however extensive and comprehensive, threatens to become merely another massive and indigestible data file, unless methods exist for easy and rapid extraction of the information. Fortunately, effective methods have been developed to a practical degree within the past few years.

Until recently, typified by Larkin and Stephen's (1971) aphorism "Formalin to FORTRAN", our manipulation of the numerical or quantified ecological representation has been constrained by computer technologies that were geared to handling rather simply structured, sequential data files. If the analytical requirements differed appreciably from the needs that were envisaged at the time the data file was structured, extensive reworking of the file necessarily preceded analysis. Sometimes it was cheaper to collect new data rather than exploit existing files.

There is now a better solution, however, with the development in recent years of a piece of computer software called the "data base management system" (DBMS). This technology offers a solution to managing the information contained in the numerical models that we have been creating in our research and monitoring activities. Going by names such as TOTAL, IMS, and System 2000, these are sets of programs, written on an exceedingly large and complex scale, that are well suited to performing a wide variety of file and data-management tasks. Developed by and for the business community, they offer the capability of handling large and complex data files, structured in hierarchies and in networks, without the necessity of getting into the difficult programming techniques necessary to handle information on this scale. In fact, most DBMS do not require programming knowledge of any kind for basic data-manipulation tasks, but make use of an English-like control language that can be learned in a matter of days. By providing independence of data from programs and transparency of the mechanics of file management and manipulation to the user, the DBMS allows investigators to consider information on the scale of primary data elements and to work with these for the most part independently of any structural constraints imposed by the data base. The availability of DBMS makes the ecological information model a practical concept.

Apart from solving the data-management problem, substantial analytical advantages also follow from the use of DBMS in conjunction with an information model. As defined by Sokal and Rohlf (1969), "data analysis" is "the systematic and largely automated scrutiny of sets of data to yield both summaries and fresh insights into the relationships in a given study." In the absence of DBMS, the simple, sequential structures of our data files do not reflect the complexity of the ecological systems they represent. Traditionally, expediency has led us to break down our problems and analyses into smaller modules that could be managed with the available technology. The effect has been that the analyses are conducted rigorously at the modular level, but become degraded to qualitative information for comparison between blocks in the structure. As a crude analogy, this might be likened to using three one-way analysis of variance tests to accomplish the analysis of a three-way factorial experiment. The point is that although the major first-order effects are elucidated in this way, second and subsequent orders of interactive effects are ignored.

The availability of DBMS allows us to depart from the simple causal approach to large-scale ecological systems by permitting the use of techniques that reveal the underlying pattern and regularities in complex information models. The problem is not unlike trying to discern the themes of an intricately orchestrated piece of music, especially if the musicians were to play in different keys. Multivariate analysis, including such techniques as factor analysis, multivariate analysis of variance, discriminate and classification functions, and canonical, multiple, and partial correlation, illustrates one class of appropriate analytical approaches. Generally, multivariate analysis achieves one or both of two objectives. The first aims at describing complex and noisy situations in more compact terms with fewer dimensions. This is basically a detection of pattern, much like that employed in clarifying images transmitted by space probes. The second objective lies in the establishment of interrelations between factors or basic components of the patterns contained in the information. Such interrelations are not easily established at once but require an heuristic approach where one is able to manipulate the conditions of the analysis, by altering the number of variables considered or by mathe-

matically rotating the solution to various degrees, to achieve a clearer interpretation. Clearly, effective application of these techniques on a large scale is greatly assisted by the use of an information model coupled with an effective data base management system. The jump in analytical capacity to be achieved by this approach is similar to that accomplished by many of us in learning to solve our quantitative problems in FORTRAN or its high-level equivalents, as distinguished from the severe analytical limitations of the ancestral, mechanical desk calculator.

Discussion

The approach we have outlined is not intended to be a global blueprint for the conduct of large-scale ecological research. Good research ultimately rests on good ideas, and no organized methodology can serve as a substitute for thinking. The information model approach can, however, serve as a useful adjunct to creative thinking by providing extensive data in an effectively usable form. In particular, our recommendations are specifically suited to large-scale governmental research and monitoring programs that are concerned with sustained utilization and management of natural resources. Voluminous data that have been collected for such programs could be of great value, beyond its initial purpose, if its availability were not impaired by the use of conventional data management techniques. In our view, the information model provides a method to extract full value from these extensive data sets.

The information model outlined by us is an unattainable ideal. It is unlikely that a comprehensive set of primary ecological variables could be assembled for a given system. Valuable approximations to the ideal can nevertheless be achieved.

The Ontario Ministry of Natural Resources has been using a data base management system called System 2000 in the development of applications in creel census, fish culture, and aquatic inventory. Using the experience gained from these projects, we are now developing a large-scale fisheries and environmental data bank, the Ontario Fisheries Information System (OFIS), based on the information model concept (Loftus 1976). If we are successful, OFIS will provide a general analytical tool for understanding fish production systems, quite apart from its direct management utility as an information retrieval package. Hopefully, we are taking a useful step beyond the FORTRAN stage discerned by Drs Larkin and Stephen.

The current objective for OFIS is to consolidate the large data backlogs from five fisheries research laboratories in different areas of the province. Subsequent collections from these laboratories, together with standard data monitored by fisheries assessment units, will provide the major continuing data inputs. Ten fisheries assessment units have been created to monitor fisheries in type areas of the province, and a further 15 or more are planned. A prototype version of OIFS is now operational, with selected sets of test data.

God may or may not play at dice — that question remains to be settled — but there is certainly every indication that He is communicating with us in an obscure code over an extremely noisy channel. But given a sufficient volume of information, no code can resist translation. We are hopefully looking toward the situation where the analyst is able to access adequate representations of large-scale ecological systems and to analyze them in such a way that major sources of variance are brought into focus quickly and investigated with comparable rapidity. Admittedly this sounds a bit like *2001*, but the technology is now available for use, and there is every indication that we need to use it.

Acknowledgments

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Phytoplankton Adaptation to Environmental Stresses from Toxicants, Nutrients, and Pollutants — a Warning

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STOCKNER, J. G., AND N. J. ANTIA. 1976. Phytoplankton adaptation to environmental stresses from toxicants, nutrients, and pollutants — a warning. J. Fish. Res. Board Can. 33: 2089–2096.

Examples are cited from the literature of phytoplankton-related pollution and nutrition studies where the possibility of successful adaptation and subsequent growth could have been overlooked because of insufficient duration of algal exposure to the pollutant or nutrient tested. We present evidence from our investigations where: a) initial algal exposures as long as 20–40 days to the pollutant or alternative nutrient may be required for successful adaptation, and b) phytoplankters initially tolerating only a low level of pollutant concentration could be trained to accept severalfold higher levels by repeated exposure to gradually increasing pollutant concentration. A plea is made for future investigators to recognize the importance of long-term bioassays ascertaining algal potential for adaptation, in order that their results may be ecologically realistic for the purpose of environmental protection against chronic pollution and eutrophication. The short-term "shock" response should be clearly distinguished from the long-term "habituation" response of phytoplankters to the test chemical in these bioassays. Possible problems raising questionable objections to the long-term bioassay approach are discussed.

STOCKNER, J. G., AND N. J. ANTIA. 1976. Phytoplankton adaptation to environmental stresses from toxicants, nutrients, and pollutants — a warning. J. Fish. Res. Board Can. 33: 2089–2096.

Les auteurs citent des exemples extraits de la littérature d'études de pollution et de nutrition touchant le phytoplancton où l'on aurait pu ignorer la possibilité d'une adaptation et d'une croissance subséquente réussies à cause d'une trop courte exposition des algues au polluant ou aux éléments nutritifs testés. Les auteurs constatent, à la suite de leurs recherches, que: a) des expositions initiales d'algues, d'une durée allant jusqu'à 20–40 jours, au polluant ou à un élément nutritif alternatif peuvent être nécessaires au succès de l'adaptation, et b) les phytoplanctontes tolérant au début seulement une faible concentration de polluant peuvent être amenés à accepter

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des niveaux plusieurs fois supérieurs par exposition répétée à une concentration croissante de polluant. Ils présentent un plaidoyer en faveur de recherches futures visant à reconnaître l'importance d'essais biologiques à long terme permettant de s'assurer du potentiel d'adaptation des algues. Les résultats de ces recherches pourront alors être écologiquement réalistes et servir à la protection de l'environnement contre la pollution chronique et l'eutrophisation. On souligne qu'il devrait y avoir claire distinction entre la réponse de « choc » à court terme et celle d' « habituation » à long terme des phytoplanctontes aux produits chimiques utilisés dans ces essais biologiques. Les auteurs examinent enfin les problèmes susceptibles de soulever des objections douteuses à la méthode d'approche d'essais biologiques à long terme.

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THE literature on experimental studies seeking to establish phytoplankton toleration of pollution stresses is full of examples that ignore the likelihood of biological adaptation. Such investigations have inferred toxic stress effects from inhibition of a) photosynthesis (measured as O_2-evolution and/or $^{14}CO_2$-fixation) after brief exposure (0.5–24 h) of microalgae to the pollutant or b) cellular growth rate measured over periods as short as 4–10 days in the presence of the pollutant. Among these investigations[1] may be cited the studies made with cobalt chloride (Blankenship and Wilbur 1975), chloroplatinic acid (Nakamura et al. 1974), lead chloride (Monahan 1973), mercuric chloride (Ben-Bassat et al. 1972), potassium dichromate (Wium-Andersen 1974), sodium selenite (Sielicki and Burnham 1973), zinc sulfate (Rachlin and Farran 1974), crude petroleum and oil-spill emulsifiers (Lacaze 1969; Boney 1970), dimethyl sulfoxide (Cheng et al. 1972), chlorinated hydrocarbons (Menzel et al. 1970; Luard 1973; Fisher 1975), DDT (Wurster 1968; Mosser et al. 1972a, b), polychlorinated biphenyl compounds (Moore and Harriss 1972; Mosser et al. 1972a, b; Fisher et al. 1973; Larsson and Tillberg 1975; Glooschenko and Glooschenko 1975), organic wastes (Hood et al. 1960), the herbicides diquat (Van Rensen 1975), aminotriazole (Wolf 1962; Siegel and Gentile 1966), Barban (Wright 1975), and other pesticides (Ellis and Goulding 1973).

Certain recommended methods for the laboratory use of algae as indicators of pollution or water quality also suffer from the drawback of not culturing the test alga with the pollutant or water sample for more than 5–7 days (Patrick 1973), an exposure period which may be insufficient for successful adaptation where possible. Even with the fastest-growing alga, we are convinced that a 15-h exposure period to a pollutant could not possibly afford scope for adaptation, and yet such a brief treatment was chosen as the basis for a growth bioassay of kraft mill effluent with an estuarine blue-green microalga (Rainville et al. 1975). We do not suggest, however, that growth recovery from adaptation would have invariably occurred with longer exposure periods than those used in the above-cited investigations, but the uncertainty, caused by ignoring the consequences of adaptation, raises grave doubts on the ecological application of these findings by environmental protection agencies. Such uncertainty is considerably diminished for the cases reported to have tested algal exposures of 14 days to several weeks, such as the studies made with mercury compounds (Nuzzi 1972; Davies 1974; Ben-Bassat and Mayer 1975), selenium compounds (Kumar and Prakash 1971), zinc chloride (Jensen et al. 1974), the acridine dye Proflavine (Kumar et al. 1967), glycerol (Cheng and Antia 1970), DDT (Bowes 1972), miscellaneous pesticides (Butler et al. 1975), naphthalene and crude oil extracts (Soto et al. 1975) and industrial wastewater from a titanium dioxide factory (Kayser 1971). This may also be true of an algal assay procedure (using 20–24 day incubations) recommended for evaluation of water quality (Payne 1975).

Evidence has recently been obtained from independent investigations involving either of us that a) certain phytoplankton species require extensive periods of exposure to certain pollutants at elevated concentrations before resuming growth and b) such adaptation enables these species not only to completely tolerate these levels of chronic pollution but to progressively increase their tolerance to gradually increasing concentrations of the pollutant. Antia and Cheng (1975) noted that two marine species of Eustigmatophyceae required about 35 days of exposure to 100 mg·liter^{-1} boron (present as boric acid) in sea water before growth was even measurable and a lag period of another 5–14 days before achieving exponential growth; this growth recovery was so complete after the adaptation that a repeat treatment of the algae with the same level of boron concentration

[1]This is not intended to be an exhaustive list but rather a selection of examples representing a wide array of pollutants, where, *in our interpretation*, the authors have been ambiguous or remiss in allowing time for adaptation.

showed growth rates and lags closely approaching those of the untreated controls (Fig. 1). These authors also observed that a) the growth performance of two marine haptophycean algae at an inhibitory boron concentration recovered gradually to its fullest extent from repeated exposure of the algae to the same pollutant concentration and b) one of these algae showed increasing tolerance to progressively augmented concentrations on successive exposure, so that pollutant levels found totally inhibitory to growth on first exposure were accepted after such adaptation (Fig. 1). Investigations of J. G. Stockner and A. C. Costella (unpublished data 1976) revealed that the coastal diatom *Skeletonema costatum* required exposures of 15 and 25 days to 20 and 30% respectively, of kraft pulpmill effluent in sea water before commencing growth, and the subsequent growth rate compared favorably with that of untreated controls, although the ultimate cellular yield was significantly depressed at the higher pollutant level (Fig. 2). This was also true of the coastal dinoflagellate *Amphidinium carteri*, which, however, required adaptation exposures of 15–17 days to 30 and 40% of the same effluent before exponential growth (Fig. 2). Our summation of these results leaves little doubt that various phytoplankton species are capable of gradual adaptation, and, therefore, greater tolerance to higher levels of pollutants than would be indicated by short-term bioassays or photosynthesis measurements, and we urge future research on water-quality protection to be ecologically realistic in recognizing the consequences of long-term adaptation leading to enhanced toleration. In fact, such adaptation may be already in progress in certain natural situations facing uncontrolled chronic pollution, since two algal isolates from smelter-emission contaminated lakes were recently reported to show exceptional heavy-metal resistance (Stokes et al. 1973). Further evidence for algal capacity to adapt toleration to foreign chemicals has been reported in connection with pharmacological studies not concerned with environmental pollution, where blue-green algae were *trained* to resist previously toxic concentrations of mutagenic and antibiotic drugs (Kumar 1964, 1965; Jain et al. 1967).

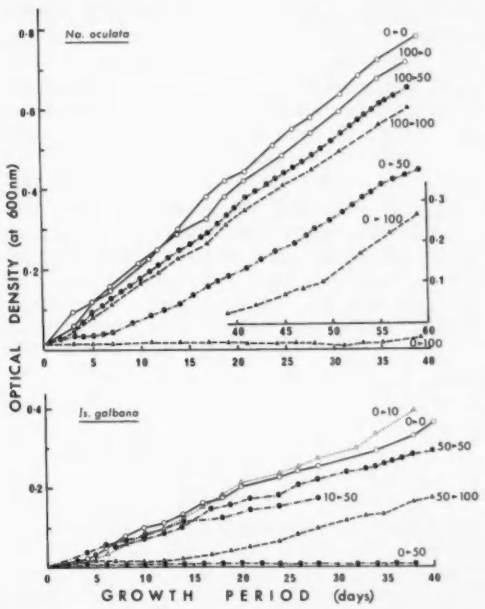

FIG. 1. Growth adaptation of the marine eustigmatophyte *Nannochloris oculata* and the marine haptophyte *Isochrysis galbana* in nutrient-enriched culture medium containing boric acid tested as pollutant. Boric acid concentrations (expressed as milligrams per liter of boron) are indicated by numerals only. Arrows show sequential exposure to the pollutant of the inoculum used in initiating each growth curve; each inoculum was taken from the mature growth obtained from the pollutant concentration shown on the left and transferred to the concentration level on the right of the arrow. For further details, see Antia and Cheng (1975).

Apart from the impact of pollutants per se, studies have been made on the effects of substances of possible nutritive value to phytoplankton in culture. Such substances may arise in situ as animal and plant excretory products (Campbell and Goldstein 1972; Hellebust 1974), or they may be introduced through domestic sewage and agricultural waste runoff, and, in the latter two cases, their concentration elevation from pollution is expected to lead to eutrophication problems (Ryther and Dunstan 1971; Filip and Middlebrooks 1976). The range of organic compounds known to be degradable (or metabolized) by planktonic algae and their potential for supporting algal growth have been comprehensively reviewed by Van Baalen and Pulish (1973) and Neilson and Lewin (1974). The former pair of reviewers have urged investigators (of the heterotrophic or eutrophication potential of such compounds) to allow the test algae ample adaptation time for modifying or renovating the metabolic machinery required for the assimilation of these compounds, and our experience compels us to emphasize this plea.

While comparing several alternative sources of nitrogen for marine phytoplankton growth, Antia et al. (1975) found that some test algae, normally accustomed to grow on inorganic nitrogen supplied as nitrate or ammonia, required adaptation periods of 2–5 wk for developing the optimal

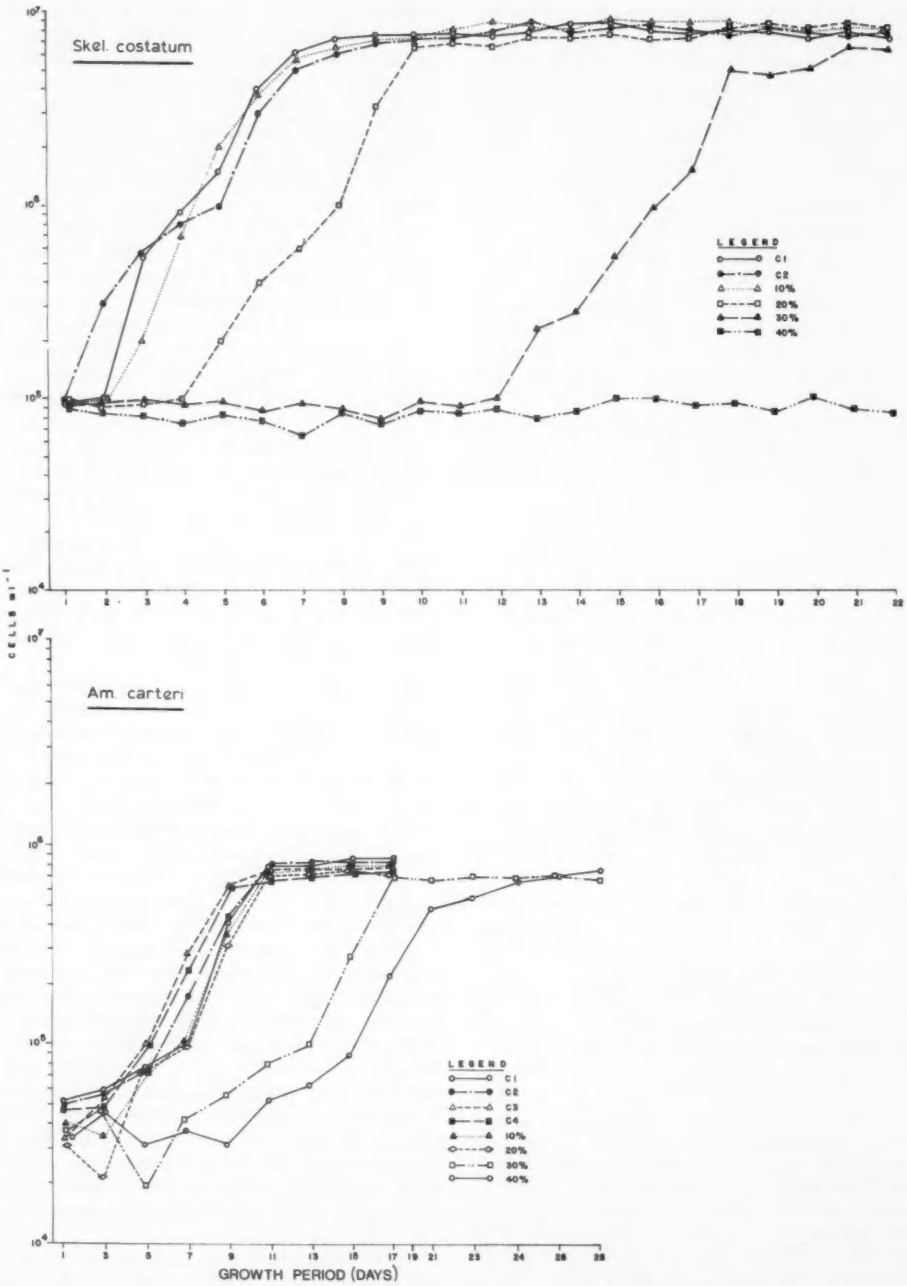

FIG. 2. Growth of the marine diatom *Skeletonema costatum* and the marine dinoflagellate *Amphidinium carteri* in various concentrations (shown as percentages) of kraft pulpmill effluent and in filtered seawater controls (denoted by C1–C4). Note the requirement for adaptation prior to commencement of exponential growth by both species, often in excess of 10 days. For further details, see J. G. Stockner and A. C. Costella unpublished data 1976).

potenial to grow on organic nitrogen supplied as the purine hypoxanthine, and, in some cases, the adaptation was so slow that growth was not measurable until 21–29 days of exposure of the alga to this compound; examples of such growth delays from adaptation are shown in Fig. 3. Furthermore, the metabolic adaptation seems considerably slower for those compounds expected to be *rarer* in the natural environment, since Landymore (1976) found that a nitrate-habituated marine diatom required no adaptation for exponential growth on the L-isomer of phenylalanine or tyrosine as sole nitrogen source but about 20 days' adaptation to develop growth on the D-isomer of the same amino acids (Fig. 4). Some of the earlier literature, concerned with similar studies on algal potential for growth on assorted organic compounds, has tended to omit mention of the time allowed for adaptation or the total duration of growth tests (Droop 1955, 1961; Birdsey and Lynch 1962; Turner 1970), and we wonder whether the negative-growth scores reported in these cases are truly valid if the possibility of adaptation was overlooked. We are similarly sceptical about the negative-growth data reported by other investigations, which appear to have used total growth periods not longer than 7–12 days after inoculation (Hayward 1965; Bunt 1969; Wyatt et al. 1971; Saito 1975). Short-term uptake measurements have frequently been used as indicators of the heterotrophic potential of various organic compounds in supporting phytoplankton growth, where the test alga is usually exposed to a compound for the first time for durations of 1–24 h (Sloan and Strickland 1966; Hellebust and Guillard 1967; McCarthy 1972; Liu and Hellebust 1974). Such determinations may be meaningful where an alga is known (or

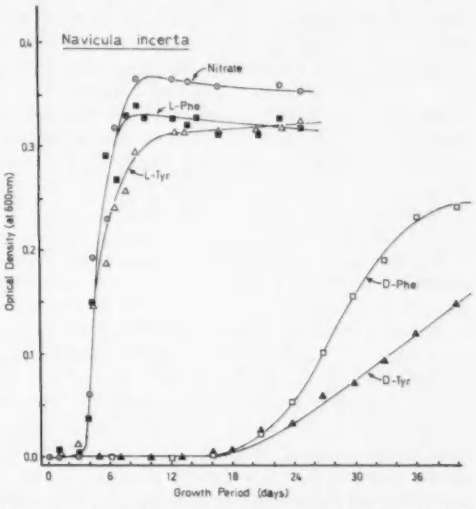

FIG. 4. Growth curves of the marine diatom *Navicula incerta* on nitrate, L-phenylalanine, D-phenylalanine, L-tyrosine, and D-tyrosine, each supplied as *exclusive* nitrogen source at a concentration of 0.5 mg-at. N·liter^{-1} to an otherwise nutrient-enriched seawater medium. Each growth shown was initiated by an equivalent inoculum taken from axenic stock cultures habituated to utilize nitrate as nitrogen source for growth and never previously treated with any of the amino acids tested. For further details, see Landymore (1976).

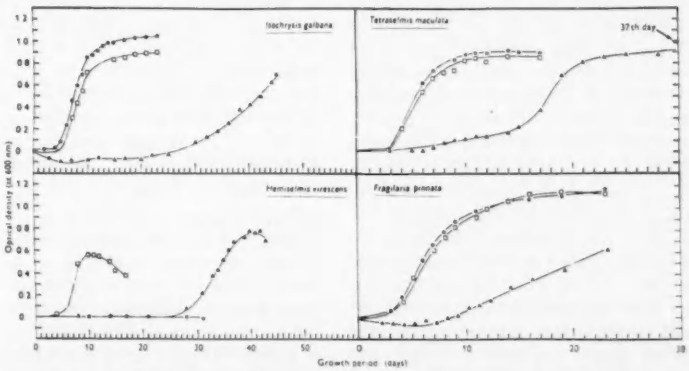

FIG. 3. Growth curves of the indicated species of marine phytoplankton on nitrate (☆), ammonium (□), and hypoxanthine (▲), each supplied as *sole* nitrogen source for growth in an otherwise nutrient-enriched seawater medium. Each nitrogen compound was added to the culture medium to give a concentration of 0.5 mg-at. N·liter^{-1}. Inoculum was always taken from axenic stock cultures accustomed to grow on nitrate or ammonium as nitrogen source and without previous exposure to externally supplied hypoxanthine. For further details, see Antia et al. (1975).

expected) to respond almost immediately to the organic substrate (within 1 day of exposure), but, in general, we find it difficult to believe that an alga, habituated to grow on one substrate, will respond so rapidly to another alternative substrate. Too little is known about the effects of adaptation and habituation on the substrate-uptake capacity of algae, but we urge caution in drawing far-reaching conclusions on the heterotrophic or eutrophication potential of an organic substrate merely from such short-term uptake results. We suggest that where poor uptake was observed from the short-term studies, the probability of improvement in this uptake should be verified after a long-term exposure permitting possible adaptation of the test alga to the substrate in question.

It behooves us to answer several objections that may be raised against our plea for the recognition of phytoplankton adaptation as stated above. In the first place, why is such adaptation so important that it cannot be ignored in some of the above-cited cases? It seems to us that the investigator concerned must decide whether (s)he is interested in a short-term "shock" response or a long-term "habituation" response of an alga to the chemical tested, and this aim should be *unequivocally stated* in order that the results may not be misinterpreted when applied or extrapolated in other directions. We admit that the short-term response would indicate the relatively *immediate* toleration potential and answer other questions of academic value, but it is only the long-term response that is expected to be ecologically realistic for application to environmental protection against pollution and eutrophication. Short-term studies may be technically convenient for laboratory and field manipulations, but Nature's philosophy has no respect for man's haste and phytoplankton in the sea and in lakes have infinite time to adapt to all forms of environmental stresses. What, then, would be a suitable experimental period for ensuring adequate adaptation of the test algae to a pollutant or an alternative nutrient? A practical compromise is required here between the limitless time available for adaptation in the natural environment and the limited time available to the investigator, who should (in our view) design studies to permit the longest possible scope for adaptation. In our experience, 30–40 days' exposure to the test chemical may be adequate to ascertain some of the most sluggish algal adaptations observed, but this will again depend on the other test conditions used (temperature and light, closed- or open-container systems, pure or mixed cultures, etc.). Furthermore, the adaptation period is expected to depend on the concentration of the test chemical and whether the alga was already exposed to it at lower concentration. However, we must caution investigators against certain artifacts and experimental limitations to the batch-assay method, problems which could be aggravated by long algal exposure to certain pollutants (see critical review of Rice et al. 1973). The long-term exposure of the pollutant or nutrient to the bioassay medium and white-light illumination could cause chemical changes of the test substance, resulting in algal-growth effects attributable to the chemically modified product rather than the original substance. Such chemical change of certain purines and pteridines promoted by seawater medium have been reported by Antia and Landymore (1974, 1975), and Lee (1973) has rightly pointed out that existing water-quality bioassay techniques have often been negligent in maintaining the proper *chemical* environment while attaching more concern to the *physical* environment. We therefore stress that a) analytical measurements should be made to know whether the proper chemical species is maintained throughout the bioassay test period or b) the bioassay alga should be resubmitted to a short-term growth assay on the test-substance, after the initial long-term adaptation to this substance, to check its postadaptation growth performance before the test substance is chemically altered to any significant extent. Examples of both types of approaches appear in the investigations of Antia and Landymore (1974, Antia and Cheng (1975), and Antia et al. (1975).

Another question that cannot be overlooked in this discussion concerns the fundamental nature of the phytoplankton adaptation observed from prolonged exposure to a pollutant or presumably unfamiliar nutrient. Is this adaptation acquired genetically via mutations or physiologically without involving the genome? This mechanistic confusion implicit in the commonly loose usage of the term "adaptation" was pointed out by Nielsen and Jørgensen (1968), who regard phytoplankton adaptation in nature to different light intensities and temperature (resulting in "sun" and "shade" phytoplankton, etc.) as physiological adjustment. Strictly speaking, however, it is not possible to answer this question without the appropriate genetic studies, although we must admit that the long-term bioassay does increase the probability of genetic change. It is not unlikely that a similar probability of genetic adaptation may apply to phytoplankton facing chronic pollution or eutrophication in the natural environment. In any case, irrespective of the mechanism involved, it would be more important to know whether such adaptation may impair the food value of phytoplankton to the next trophic level in the aquatic food web.

This consideration leads us to a final question. Assuming phytoplankton to be capable of continuous adaptation to rising concentrations of pollutants, what concentration levels should environment protection agencies accept as the ultimate cutoff point for a contaminant? In view of the known capacity of aquatic fauna to accumulate the toxic chemicals from their plant foods, our food-web perspective anticipates that the toleration degree of the feeders (including man as the ultimate predator) should logically govern this cutoff point, which, we suspect, may lie considerably below the adaptation potential of phytoplankton.

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Science for Canada's Atlantic Inshore Seas Fisheries[1]

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Contents

2098 ABSTRACT

2098 RÉSUMÉ

2100 PART I INSHORE SEAS FISHERIES
2100 Inshore seas identified and defined
2100 Identification of the inshore fisheries problem
2101 Dimensions of the problem
2105 Fish resources and use in two selected areas

2111 PART II PAST AND PRESENT SCIENCE EFFORT
2111 Fisheries science, statistical gathering mechanisms, and extension
2114 State of knowledge of natural resources in two selected areas

2121 PART III AN ANALYSIS
2121 Scientific activities and regional development
2124 Alternative development strategies for regional economy and inshore fishing communities
2126 Congruence of issues

2127 PART IV SOCIAL SCIENCE NEEDS AND COMMUNITY INITIATIVES
Social science-related activities and fisheries resource management
2131 Identifying community alternatives

2133 CONCLUSIONS AND RECOMMENDATIONS

2135 ACKNOWLEDGMENTS

2135 REFERENCES

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Abstract

McCRACKEN, F. D., AND R. S. D. MACDONALD. 1976. Science for Canada's Atlantic inshore seas fisheries. J. Fish. Res. Board Can. 33: 2097–2139.

This study is a sequel to "Science for Canada's Shelf Seas Fisheries" by Regier and McCracken (1975).

Inshore seas fisheries cannot be defined rigorously and only acquire meaning on the Atlantic coast where there are many weakly organized fishermen based in about 2000 communities.

This paper attempts to identify the science effort necessary to help resolve the problem of making decisions about many small fisheries-based communities. Particular attention is paid to the east coast of Newfoundland and Labrador and the Gulf of St. Lawrence.

Science effort has not been related to an inshore–offshore seas relationship, and there is little difference in natural science needs between inshore and shelf-seas fisheries, with the exception of research on such important invertebrates as lobster, local mapping and monitoring of invertebrates, studies on seaweeds, and development of a viable extension service. An understanding of the cod–capelin–mammal complex off the east coast of Newfoundland and Labrador is urgent. Managing the aquatic resources of the Gulf of St. Lawrence on a multiple-use and multiple-species basis has high priority.

These science needs are seen in the perspective of a manipulative sociopolitical subsistence system which perpetuates high unemployment, low income, and much dependency on government; and of three broad policy options. The only untried option aims for a balanced corporate–noncorporate fishery and attempts to counter the manipulative system by suggested measures which promote equity, productivity, and creativity. A broad congruence of issues on an international scale points to greater theoretical acceptance of this option; however, the greater degree of material sacrifice may not be acceptable to those affected.

If this course is followed, demand to resolve the natural science problems identified above will be much greater. Social science activity will also have to change direction towards (a) more interdisciplinary study and input in decision-making, (b) more emphasis on innovation rather than analysis, (c) more countervailing sources of expertise. Community development is of critical importance in its role of stimulating self-help and of being a mirror image of corporate planning.

It is essential to greatly increase inshore fisheries representation in fisheries decision-making. Some principles developed in this paper may also apply to other areas where rural communities suffer encroachments from corporate interests.

Résumé

McCRACKEN, F. D., AND R. S. D. MACDONALD. 1976. Science for Canada's Atlantic inshore seas fisheries. J. Fish. Res. Board Can. 33: 2097–2139.

Cette étude fait suite à l'article de Regier et McCracken (1975), «Science pour les pêches canadiennes dans les mers du plateau continental».

Les pêches des mers côtières ne peuvent être exactement définies : elles n'ont une signification réelle que sur la côte de l'Atlantique où se trouvent un grand nombre de pêcheurs assez peu organisés, groupés dans quelque 2000 centres.

Le présent article veut identifier l'effort scientifique nécessaire à la solution du problème de prise de décisions touchant plusieurs petites communautés axées sur les pêches. Nous accordons une attention particulière à la côte orientale de Terre-Neuve et du Labrador et au golfe Saint-Laurent.

L'effort scientifique ne se rattache pas à une relation mers côtières–mers du large. Il y a d'ailleurs peu de différence dans les besoins en sciences naturelles entre les pêches côtières et celles des mers bordières, à l'exception de la recherche sur d'importants invertébrés tel le homard, de la cartographie et du contrôle suivi, localement, des invertébrés, d'études sur les algues et du développement d'un service de vulgarisation viable. Il faut de toute urgence comprendre le complexe morue–capelan–mammifères au large de la côte orientale de Terre-Neuve et du Labrador. On devra accorder une haute priorité à la gestion des ressources aquatiques du golfe Saint-Laurent, gestion fondée sur l'utilisation diversifiée d'espèces multiples.

Nous envisageons ces besoins en science dans le contexte d'un système de subsistance socio-politique de tripotage qui encourage un chômage chronique, de faibles revenus et une forte dépendance du gouvernement; et dans le contexte de trois options de politique générale. La seule option qui n'a pas encore été éprouvée vise à établir une pêcherie corporative–non corporative équilibrée et tente de remédier à l'actuel système de tripotage en suggérant des mesures destinées à promouvoir la justice, la productivité et la créativité. La conformité des problèmes qui se posent à l'échelle internationale fait prévoir une plus grande acceptation théorique de cette option;

cependant, les sacrifices matériels accrus qu'elle comporte peuvent ne pas être acceptables à ceux qui sont affectés.

Si l'on s'engage dans cette voie, on devra s'attendre à ce que la demande de solution aux problèmes de sciences naturelles mentionnées plus haut se fasse plus pressante. Les sciences sociales devront également changer de direction et s'orienter vers (a) une approche plus interdisciplinaire à la prise de décisions, (b) plus d'accent sur l'innovation plutôt que sur l'analyse, (c) davantage de sources d'expertise qui se contrebalancent. Le développement communautaire, dans son rôle de stimulant aux efforts personnels et de contrepartie à la planification corporative, est d'une importance critique.

Il faut de toute nécessité permettre aux pêches côtières d'être beaucoup mieux représentées dans le processus de prise de décisions. Certains principes énoncés dans cet article peuvent également s'appliquer à d'autres domaines où les intérêts corporatifs empiètent sur les communautés rurales.

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There is no such thing as the viability of states or of nations, there is only a problem of viability of people: people, actual persons like you and me, are viable when they can stand on their own feet and earn their keep. You do not make non-viable people viable by putting large numbers of them into one huge community, and you do not make viable people non-viable by splitting a large community into a number of smaller, more intimate, more coherent and more manageable groups.

E. F. SCHUMACHER (1974)

The subsistence fishing and farming bit is too impractical these days except for capricious well-to-do retirees or romantically-minded urban youths — and the latter panic at first snowfall anyway ...

Oh you're goin' fishin' like your daddy fished before are you?

Nothing big like a longliner. Just a punt and a jigger. A few lobster pots and a salmon net.

Oh, my poor man! Have you ever got another think coming. That sort of fishing is more complicated, more demanding of skill, experience, ability, lore and luck than putting together atomic bombs in a snowstorm in the dark.

These so-called "poor humble fishermen" had to have more knowledge tucked away in their weather-beaten skulls than a jet pilot has.

Nope, this inshore fishing racket is an exquisite art and no good for the likes of you or me to think we could master it in half a lifetime.

R. GUY (1975)

All the vicissitudes with which the fishing industry has had to contend might well be summarized under the twin rubrics of "fish or no fish," "good markets or bad ..."

The former circumstance is one that will not surprise anyone who is even remotely aware of what has been happening in the North-west Atlantic during the past three decades. The profligate, if not actually criminal, manner in which we have permitted depletion of what ought to be an infinitely renewable resource will probably rank as one of the great asininities of the twentieth century. While such intemperate language may be considered inappropriate to a dispassionate and sober board of conciliation, it is difficult to be restrained in the face of a potential ecological disaster which is not only predictable but which is preventable.

REPORT OF THE CONCILIATION BOARD (1974)

Part I. Inshore Seas Fisheries

Inshore Seas Identified and Defined

In this study, which is a follow-up to "Science for Canada's shelf-seas fisheries" (Regier and McCracken 1975), we propose to identify the inshore seas as the marine part of a specific type of coastal zone (a zone of interaction between all humanities, whether land- or sea-based). Although coastal zones are rarely defined in precise terms (Federal–Provincial Coastal Zone Review Committee 1975; Johnston et al. 1975), they may be classified into two major types:

1) A coastal zone with a high degree of modernization, economic and community differentiation, and the interaction of organized interests. The B.C. coastal zone is representative of this type. Here the issues are more connected with the integrity of the physical environment in the face of a high degree of economic development.

2) A coastal zone with both modern and traditional sectors, as on the Atlantic coast. This represents the interactions between the more organized and specialized, higher income economic interests and those less well organized. The latter have less specialized roles and less cash income, and few local resource development alternatives. It also represents major interactions among those in each category. Here the issues are more related to the social and cultural diseconomies of economic growth.

It is the latter type of coastal zone that we define as inshore seas, and the most noticeable aspect is the conflict between different types of fishermen for the same limited resource. The inshore fisherman is based in hundreds of communities along the coast whereas the offshore fisherman is based in only a few fishing centres. This conflict may be directly between fishermen within the inner zone, whether related to the resource or the fishing method, or indirect when fishing "offshore" affects the inshore resource.

Inshore versus offshore distinctions are meaningless in the first type of coastal zone. This is largely because most fishermen are equally mobile and organized and are mainly based in a few urban settlements with a large range of full-time and specialized alternatives. Also, the fisheries are less important to the regional economy.

Our definition "inshore seas" are those accessible to inshore fishermen as well as offshore fishermen. In the Atlantic coast context we have arbitrarily classified an inshore fisherman as one who fishes in a vessel less than 100 feet long as there are few company-owned vessels in this size range (about 100). "Inshore seas" can then be regarded roughly as a 50-mile band of water around the Atlantic coast plus the Bay of Fundy and the whole of the Gulf of St. Lawrence (see Fig. 1).

In this study we have chosen two specific inshore seas areas for particular attention: (1) the east coast of Newfoundland and Labrador (Cape St. Mary's to Hopedale), and (2) the Gulf of St. Lawrence (see Fig. 1). Both areas have a large number of fishermen and communities in relation to other areas, and are models for resolving fisheries and multiple-use conflicts, but there is at the same time an important difference. The Gulf of St. Lawrence is now close to being a Canadian inshore sea, while the east coast of Newfoundland and Labrador is a model of allocating fish stocks between inshore and domestic and foreign offshore interests.

Identification of the Inshore Fisheries Problem

The Problem of the Inshore Fisheries on the Atlantic Coast

The Atlantic coast inshore seas fisheries problem is whether and how to maintain, enhance, or destroy independent or dependent ways of life found in hundreds of small communities where fisheries activity is critical to community viability and to the regional economy. Also, it is the question of who makes the decisions and what the processes of asking and solving these questions are.

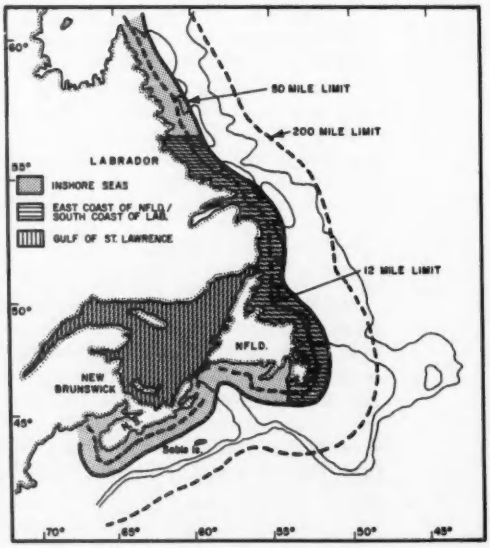

FIG. 1. Inshore seas.

This problem is not new but the need for its resolution has recently been accentuated by (a) growth of offshore and foreign fleets in relation to stable or dwindling fish stocks, (b) more efficient inshore technology, and (c) the apparently increasing urbanization and modernization in most other areas of Canada.

What are the social and natural sciences needs, if any, to help resolve the inshore fisheries problem? — Despite differences to be found in British Columbia, many principles drawn from our study of the Atlantic coast might apply to Indian and other rural communities in B.C. This is because Atlantic coast inshore fisheries are an extreme example of problems of a rural hinterland drained by the urban centre. They might also apply to the Arctic coast and freshwater fisheries as traditional rural communities suffer encroachments from intruding corporate interests.

Dimensions of the Problem

Fisheries Contributions to Regional Economy

The fisheries sector contributes as follows to value added in each of the Atlantic coast provinces (1972 figures) (Source: Annual Statistical Review of Canadian Fisheries, Vol. 7, 1974)

	$ Million	% of all commodity producing industries
Nova Scotia	113.3	13.3
New Brunswick	41.5	5.9
Prince Edward Island	15.9	16.6
Newfoundland	77.1	12.6
Atlantic Provinces total	247.8	11.0
Quebec	23.5	0.2
Atlantic coast total	269.3	2.2

Employment figures for fishing and fish-processing activities in relation to total employment (1973) were as follows: (Source: Annual Statistical Review of Canadian Fisheries, Vol. 7, 1974)

	Fisheries	Total employment	%
Newfoundland	21,000	159,000	13.2
Maritimes	28,000	519,000	5.39
Atlantic Provinces Total	49,000	678,000	7.23
Quebec	7,000	2,375,000	0.029
Atlantic coast	56,000	3,053,000	1.83

Fisheries in Canada contributed 1% to value added (1972), and employed 80,000 out of a total labor force of 8,816,000 (1973). Thus, although the fisheries sector does not appear to be important to Canada as a whole, it takes on real significance to regional economies on the Atlantic coast.

Numbers of Communities

Fisheries activities, in particular inshore fisheries activities, are even more significant at the micro-regional or community level. The 1971 Census showed 964 communities in the Atlantic coast region which includes Newfoundland, Prince Edward Island, Nova Scotia, New Brunswick, and the St. Lawrence and Gaspé areas of Quebec. Of these, approximately 702 communities were dependent to some degree on fishing or fish processing. Communities which have some dependence on fishing are distributed as follows: (Source: Department of the Environment, Fisheries and Marine Service)

Newfoundland	273
Prince Edward Island	94
Nova Scotia	87
New Brunswick	136
Quebec	112
Total	702

The Census definition of communities is almost meaningless, as there are often several landing points and settlements to each community as defined by the Census. For instance, in Newfoundland there were 745 landing points and 615 settlements (1971 figures) reported, and there are approximately 1400 other settlements to be found in the other Atlantic coast provinces making a total of about 2000.

There is a wide range of community sizes and types, from the Halifax–Dartmouth metropolitan area with a population of close to a quarter of a million to small settlements of less than 50 persons. Of these communities approximately 30 might be classed as offshore fisheries-based communities with groundfish landings of over 1 million pounds. About 50 of the inshore fishery communities have fish landings valued in excess of $500,000.

It is the lack of community differentiation (the diversity of employment categories present in the community), and of alternative natural resources or employment opportunities for a large proportion of the Atlantic coast inshore fishery communities which was identified by the 1975 Groundfish Task Force as the crucial factor in determination of average income and growth prospects for a community. This is supported by Table 1.

The figures should be treated with caution as there is normally a large portion of undeclared income in rural communities in the form of cash,

TABLE 1. Average household income in fishing and all communities by province, 1971. (Source: Groundfish Task Force 1975)

	NFLD.	N.S.	N.B.	P.E.I.	QUE.
Number communities with fishing and/or fish processing as first or second employer	142	26	28	37	14
Average household income	$4901	$6364	$5972	$5450	$6194
Number communities with some employment in fishing	134	60	104	57	86
Average household income	$5612	$7090	$6658	$6298	$6967
Provincial average household income, all communities	$7220	$7927	$7583	$6970	$9086

TABLE 2. Atlantic sea fisheries: catches and landed values of principal species, by groups, 1966–74. Nominal catches, Q, in metric tons, live weight; landed values, V, in thousand dollars. (Source: Ann. Stat. Rev. Can. Fish., Vol. 7, 1974)

		Groundfish	Pelagic, estuarial	Shellfish	Total
1955	Q	486,499	135,347	42,298	664,144
	V	24,484	6,289	18,186	48,959
1961	Q	467,054	108,813	72,463	648,330
	V	28,523	6,842	22,081	57,446
1967	Q	589,838	374,727	76,102	1,040,667
	V	28,523	16,352	32,623	98,059
1973	Q	539,926	273,623	74,929	888,478
	V	80,724	23,597	63,232	167,553
1974[a]	Q	417,763	277,698	85,499	780,960
	V	73,863	25,728	64,025	163,616

[a]Preliminary figures.

in terms of barter transactions and payments in kind, and in terms of public goods and psychic income (from the built-in advantages of rural living, e.g. solitude, outdoor recreation values etc.). Discrepancies between rural and urban incomes should also be considered in relation to cost of living differences between rural and urban areas. Living costs are usually significantly less in rural areas due to lack of mortgage and rent payments on houses and other forms of cost savings.

Community differentiation is enhanced if there are fish processing plants or large vessel operations, and by the availability of other resources or employment opportunities and subsidies. (The degree of government assistance for Newfoundland was well documented by Copes (1972).) Access to other natural resources, e.g. forests, has decreased due to increased use of capital–intensive technology and the resulting decline in demand for labor in primary extraction.

Unemployment insurance subsidies, welfare, and the other forms of social security are also important alternative resources to these communities. For instance, in the Atlantic coast area over $14 million unemployment insurance benefits were paid to fishermen between Dec. 1, 1973, and May 31, 1974.

FISHERIES RESOURCES

Some measure of aggregate fish resource availability on the Atlantic coast may be gathered from Table 2.

The salient points, i.e. increases in catches in the early 1960s, a peak catch in 1967 (actually the peak was in 1968), and declines since, accompanied by a steady upward movement in landed value followed by a decline for groundfish in 1974, are already well known. Indeed the unprecedented decline in fish supply accompanied by an overall cost squeeze, and fall in demand in 1974, were the key features that caused the crisis in the groundfish industry. This has led to large "bridging" measures and rehabilitation plans on the part of government.

Fishermen and Their Vessels

Pursuing these resources on the Atlantic coast are some 39,000 fishermen of whom approximately 36,500 are inshore fishermen. In 1973 there were about 15,500 in Newfoundland, 5500 in Quebec, 2500 in Prince Edward Island, 5000 in New Brunswick, and 10,500 in Nova Scotia. Up to now, due to low capital investment required in small boats and to unlimited access to the resource, many inshore fishermen have been able to enter and leave the fishery with ease. (Entry permits are now required in the following fisheries: salmon, herring, lobster, scallops, and snow crab. In the groundfish fishery, vessels over 45 feet long require entry permits.) In times of general prosperity many fishermen have found jobs elsewhere but have traditionally returned to the fishery when unemployment rates were high (Copes 1972). This accounts for some fluctuation in numbers prior to the late 1960s.

In 1972, about 5500 fishermen on the Atlantic coast were classified as full-time, about 14,000 as part-time, and about 20,000 as occasional. Almost all the 2500 offshore fishermen fall under the full-time category. These figures give some indication of the seasonal nature of the inshore fishery, and the degree of occupational pluralism which is such a key characteristic of the less-differentiated communities in the area. (For instance, in Newfoundland the maximum duration in months of the fishing season varies between 5–5½ for southern Labrador and 12 for the coast between Cape Race and Cape Ray (Copes 1972). In the Gulf of St. Lawrence this varies between 8 months for the northeastern Gulf to 9–11 months for different areas of the southwestern Gulf.) Although occupational pluralism has been in decline in most countries, the figures for part-time and occasional fishermen for the Atlantic coast provinces do not bear this out over the 1970–73 period (Annual Statistical Review of Canadian Fisheries 1974). Where occupational pluralism occurs, it is more relevant to consider the economy of the whole household and its place in the community rather than the economy of the fisheries sector, when attempting to understand the social and economic behavior of inshore fishermen and when planning (Brox 1972). Unfortunately there is a dearth of good information describing the productive role of occupational pluralists in detail (Andersen 1974), their entrepreneurial abilities, and potential for individual and community initiatives (Park 1973). Occupational pluralism is not unique to Canada's Atlantic coast. For instance, Andersen (1974) states that 35% of the fishermen labor force in Sweden were occupational pluralists in 1968, about 25% in Denmark, 55% in Norway in 1966, and 70% in Ireland in 1966. Income from occasional and part-time fishing on the Atlantic coast plays a far more crucial role to total household budget than the low per capita income figures would superficially indicate (Brox 1972), and social security and unemployment insurance have recently replaced gardening, and other part-time productive activities.

Diversification between species and species groups within the inshore fishery is common and the following figures (for the total number of fishermen on the Atlantic coast, i.e. persons engaged in more than one fishery are duplicated) for 1973 demonstrate this: (Source: Annual Statistical Review of Canadian Fisheries, Vol. 7, 1974)

	No. fishermen
Groundfish	21,572
Herring	12,111
Lobster	20,418
Mackerel	5,687
Salmon	5,979

Inshore fishermen are characterized by being weakly organized into unions or associations. In the Atlantic coast area there are approximately 40 exclusively fisheries organizations, often with little more than 20 members, but some such as the Newfoundland Fishermen Food and Allied Workers (NFFAW) claim a membership of 6000 divided into 1000 offshore and 5000 inshore fishermen. Forty-one % of fishermen on the Atlantic coast belong to formal organizations versus 68% on the Pacific coast (R. E. Quirt, unpublished data). Strength of the unions appears to be growing but whether it will be mainly an offshore fishery–processing labor phenomenon remains to be seen. The NFFAW and the Atlantic Fishermen's Association (membership 1000) are the newest large organizations. The older United Maritime Fishermen Ltd. is a cooperative with 35 active member coops with an approximate membership of 3500. The variety of organizations is indicative of a certain identification problem. Some fishermen see themselves as businessmen, others as labor to be organized into unions, and others as members of cooperatives.

Overall value of fishing craft on the Atlantic Coast in 1972 was close to $165 million; of this, approximately $65 million might be attributable to inshore vessels of less than 100 feet (or more strictly speaking less than 150 tons). Current investment (1972) in fishing gear (offshore and inshore) was of the order of $6 million in Nova

Scotia, $2.6 million in New Brunswick, $0.5 million in Prince Edward Island and $1.3 million in Quebec. The total value of gear inventory in Newfoundland was $13.3 million.

Studies such as "Costs and earnings of selected enterprises, Nova Scotia 1974" (Anon. 1975a) tend to indicate that vessels less than 100 feet long have better profit and loss performance vis-a-vis vessels of more than 100 feet; however, these figures are not conclusive because of the small sample and the variability of fishermen, vessels, and conditions. Evidence from Newfoundland and elsewhere tends to point to the superior economic performance of vessels less than 100 feet.

Harbor Infrastructure

Inshore fishermen have not always settled close to good harbors, particularly for larger craft. Major historical reasons for the extreme case of Newfoundland were (1) accessibility to the natural resource, (2) use of small boats which could be hauled up on any beach, (3) the need to avoid arrest for illegal settlement prior to 1824 and up until the turn of this century for the "French Shore," and (4) the need for large acreages of shore front for flakes.

These unique historical factors have led to a situation in Newfoundland where many communities are unable to use conventional modern large craft technology due to lack of harbor potential. In the past, due to political considerations, ridiculous efforts were made to create expensive harbors in impossible situations for only a handful of fishermen, when more imaginative use of alternative technology, commuting, or relocation might have been more appropriate.

The problems of Newfoundland in this respect are an extreme example of many situations in the Atlantic coast area generally. A key aspect is that it has become traditional for the federal government to provide small craft harbors without relation to any financial responsibility by local communities, and the political and policy ramifications of this are spectacular. (For a decision on criteria for port location and development see Anon. 1974.)

A small craft harbors system study, completed in 1974, identified 101 developable harbors in Nova Scotia, 64 suitable for inshore fisheries only (i.e. for vessels of less than 25 tons). Thirty-five developable harbors were identified in New Brunswick, 25 suitable for inshore operations only. Eighteen developable harbors were identified in Prince Edward Island, 16 suitable for inshore operations. In Newfoundland 107 communities had sufficient harbor development potential to be rated on a 1 to 8 scale. Under the 1968 Canada–Quebec Agreement, 2 principal fishing centers, 3 auxiliary centers, and 17 collection points were identified for the Gaspé and the Iles-de-la-Madeleine. The criterion of what is "developable" in all cases is related to conventional vessel and infrastructure design and technology — the degree to which "developability" could change due to innovations is difficult to establish.

Fish Processing, Marketing, and Markets

Fish processing, marketing, and markets are extremely important to inshore fisheries communities and management of inshore marine resources. These determine the nature of the demand for fish products, and the degree to which the potentially volatile derived demand for the resource fluctuates in relation to end-market prices.

In general the structure and behavior of the processing industry has been such that it has had little control over end-market prices (mainly in the U.S.), but a high degree of control over prices to fishermen. There has thus been a tendency for derived demand for landed fish to be dampened on the up-turn. These historical patterns have been changed to some extent recently due to the impact of unionization, subsidy programs, and in the Newfoundland context, from the Canadian Saltfish Corporation. As a result, landed fish prices have risen to a higher level without any drop-back to the former low plateau. (Annual Statistical Review of Canadian Fisheries 1974.)

Another dominant feature of the fish processing industry is its instability due principally to lack of control over end-markets, to lack of guarantees of fish supply due to foreign fishing pressure, and to the inherent lack of predictability of fish supplies. All this has been accentuated by government subsidies and interventions which appear to have often contributed to a 6-year cycle of boom or bust since World War II.

There are over 300 fish plants in the Atlantic coast region employing 16,640 persons (1973 figures). Employment was distributed as follows in 1972: (Source: Department of the Environment, Fisheries and Marine Service 1974)

Nova Scotia	5,351
New Brunswick	3,337
Prince Edward Island	685
Quebec	1,296
Newfoundland	5,971
Total	16,640

This compares with a Canadian total of 21,424.

The number of fish plants belies the degree of concentration in the industry. For instance, the offshore fleet, owned by about 12 companies, takes 70% of the groundfish catch on the Atlantic coast. Generally there is excess capacity and overcapitalization in relation to the resource base.

In 1973 the Atlantic coast fishing industry produced close to $450 million worth of fish products. About $160 million was sold in frozen block or fillet form; $95 million of shellfish in shell or shucked, fresh, or frozen; $54 million in fresh filleted or whole form; $40 million in canned form; $42 million in salted, cured, or smoked form; and $23 million in meal and oil. An arbitrary estimate of inshore fisheries contribution (i.e. excluding trawler contributions) to this total is about $250 million. A major proportion of these products is exported, mainly to the USA. For frozen groundfish products, 55–60% of total production on the Atlantic coast is exported to the USA and handled by 30 exporters, only 3 of which are integrated into that market.

Direct per capita fish consumption in the US and Canada is stable and low (in Canada 12.1 pounds in 1973), but little has been done by industry as a whole to organize marketing, improve quality control procedures and sales promotion techniques, and to find alternative export markets and ways to enhance the value-added. This is partly due to international tariffs and trade arrangements, and to the nature of the Atlantic coast industry.

In short, inshore fishery communities are separated from their final products markets by an industry which appears to have most disadvantages of concentration and most drawbacks of fragmentation. Both federal and provincial layers of government have tended to indulge the industry in its weaknesses even though problems and their solutions have been repetitively identified for years by public and internal government reports (Atlantic Provinces Economic Council 1974).

Fish Resources and Use in Two Selected Areas

East Coast of Newfoundland and Labrador

This area is delineated in Fig. 1, and represents those inshore seas within ICNAF divisions 2J and 3KL (see Fig. 2).

Labrador — In 1956 prior to intensification of the offshore fishery the primary resource base for the inshore Labrador fishery was cod with salmon providing an important cash crop (Fig. 3). By 1972 and 1974 (Fig. 4) offshore fishing

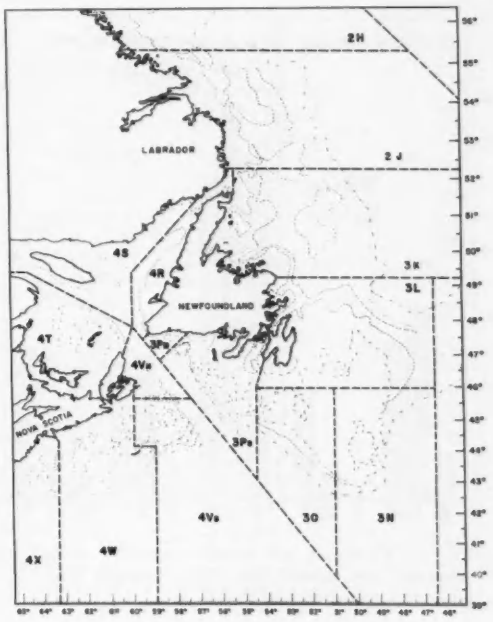

FIG.2. ICNAF fishing areas.

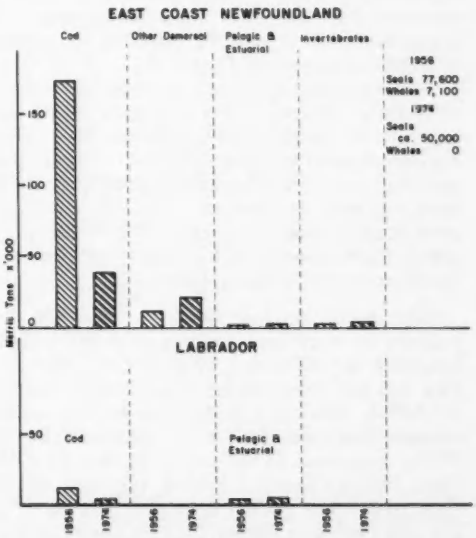

FIG. 3. Canadian landings; all species, Labrador and east coast Newfoundland 1956 vs. 1974.

for cod (foreign vessels) had increased by 5 or 6 times and capelin were also being exploited heavily. The inshore cod fishery had declined from about 10,000 tons to slightly less than 2000

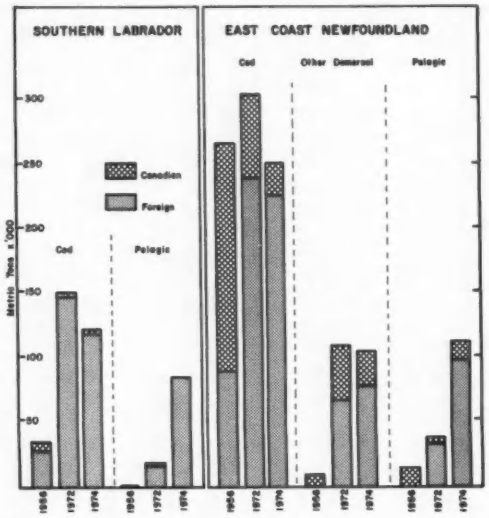

FIG. 4. Canadian and foreign nominal catches of demersal and pelagic fish from southern Labrador and east coast Newfoundland.

tons (about ⅛ the 1956 landings), and combined salmon and pelagic catch provided a greater landed value than cod. Total landed value of about $1.2 million in 1972 provided an average of $1400 per fisherman (Table 3).

A comparison between the years 1956 and 1972 (latest figures readily available) shows that numbers of fishermen, and sophistication of their equipment has increased (Table 4). This is particularly true for the increase in gasoline powered boats, gillnets and salmon nets. However, the most marked change is in the offshore fishery in which Canadians are not currently participating except on an experimental basis.

East coast Newfoundland — In 1956 the primary resource base was cod of which inshore fishermen landed about 170,000 tons (Fig. 3). This was supplemented by much smaller catches of flatfish, herring, capelin, lobster, and squid. Inshore fishermen also took a portion of about 7000 whales and 75,000 seals. At that time offshore fishing (foreign) landed only cod and in 1956 took about 90,000 tons (Fig. 4). By 1972 and 1974 offshore fishing for cod (foreign) had increased between 2 and 3 times to about 225,000 tons (Fig. 4). Foreign vessels were also exploiting other demersal species, landing about 10,000 tons. In addition an intensive fishery for capelin begun in 1972 took at least 250,000 tons in 1974 (including Labrador).

In contrast, the Canadian cod fishery, mainly inshore, had declined from 170,000 tons recorded in 1956 to about 65,000 tons in 1972 and to 35,000 tons in 1974. Landings of other demersal fish had increased slightly, from about 16,000 to 22,000 tons. Snow crabs had been added to the invertebrate resources with landings of about 2000–3000 tons. East coast Newfoundland fishermen have not participated in the development of the capelin fishery.

While the number of inshore fishermen had decreased slightly, from 8900 in 1956 to 7400 in 1972 (this decrease may not be significant as there have been marked fluctuations in numbers of fishermen from year to year), their vessels and gear tended to be upgraded, e.g. a 14-fold increase in number of longliners, a 15 times increase in cod gillnets, and a marked increase in number of salmon nets and lobster traps (Table 4). Technological developments within the inshore fleet have provided increased competition. Total landed value of about $11.8 million in 1972 provided an average income of about $1600 per fisherman (Table 3).

SUMMARY

In brief, a number of items stand out: (1) 19% of the fishermen on the Atlantic coast or 12% of Canadian fishermen are fishing off the northeast coast of Newfoundland and south coast of Labrador; (2) success of the inshore cod fisheries off Labrador and east coast Newfoundland depends greatly on what happens in offshore fisheries. Not only is cod being exploited heavily there, but a rapidly developing offshore capelin fishery of major proportions adds a new dimension of complexity; (3) the seasonal inshore fishery is markedly influenced by natural weather cycles which include both ice conditions and presumably water temperature; (4) there has been some reduction in number of fishermen engaged in the inshore fishery, but a marked upgrading of technology of boats and gear; and (5) invertebrate resources fished are almost entirely confined to lobsters and crabs.

GULF OF ST. LAWRENCE

This area is delineated in Fig. 1 (for ICNAF Division see Fig. 2).

The Gulf of St. Lawrence is partly separated into a southwestern section (ICNAF Division 4T) and a northeastern section (ICNAF Division 4R and 4S) by the Laurentian Channel. The northeastern section is partly divided again by the Esquiman Channel, extending toward the Strait of Belle Isle.

TABLE 3. Average value of landings/fisherman for east coast of Newfoundland and Labrador and the Gulf of St. Lawrence (B.C. for comparison) 1972 figures.

Area	Total landed value (ρ 000)	No. fishermen	Avg. landed value/fisherman ($)
Labrador	1,210	863	1,400
East coast Nfld.	11,800	7,400	1,600
Gulf of St. Lawrence			
W. coast Nfld.	4,500	2,500	1,800
N. shore Quebec	1,116	1,600	697
Gaspé & Magdalens	9,584	3,500	2,738
Northern N.B.	10,876	3,837	2,834
Nova Scotia	3,913	1,483	2,638
Prince Edward Island	10,100	3,200	3,100
	53,000	24,200	
British Columbia	75,100	9,900	7,600

TABLE 4. Newfoundland: fishermen, vessels and gear, 1956 vs. 1972.

	East coast Nfld. 3KL		Labrador 2J	
	1956	1972	1956	1972
Fishermen				
Inshore[a]	8,900	7,315	733	863
Offshore	75	83	0	0
Full time	75	83	0	0
Part-time & occasional	8,900	7,315	733	863
Vessels				
Trawlers	3	3	0	0
Draggers	3	0	0	0
Longliners > 25 tons	19	83	0	0
Longliners < 25 tons	6	265	0	7
Boats (row)	3,311	842	225	47
Boats (gas)	4,332	4,060	380	706
Gear				
Gillnets (pelagic)	3,700	3,500	0	740
Gillnets (cod)	2,300	37,000	4	1,600
Nets (salmon)	4,800	7,900	1,850	2,800
Seines (pelagic)	480	105	0	25
Traps (cod)	1,990	1,660	224	300
Lines (trawl)	50,000	19,500	3,600	4,200
Lines (hand)	13,300	6,500	600	600
Traps (lobster)	114,000	155,000	0	17
(crab)	0	?	0	?

[a]Categorized from type of fishing for 1956–72. (Fish. Stat. Can. 1956, 1972)

Commercial fisheries — Current Canadian fish landings from the Gulf of St. Lawrence include a large number of species (Table 5). In the southwestern Gulf, cod, small flatfish, herring, and seaweeds contribute most in volume of landings. However, in value, invertebrates, particularly lobsters, snow crabs, and scallops, contribute nearly 60% of the total. Seaweeds also contribute strongly to landings.

In the northeastern Gulf species utilized are not as numerous as in the other half and redfish, cod, and herring make up the bulk of landings (Table 5). Demersal species contributed 57% of the value and invertebrates only 19% in 1974. Of invertebrates, shrimp was the most important species landed.

Recreational fisheries — Although tourism is expanding in the region, there has not yet occurred the remarkable growth in sports fishery as

TABLE 5. Landings by species and estimated values of Canadian landings from the southwestern and northeastern Gulf of St. Lawrence in 1974. (Data from ICNAF Stat. Bull. 24. Values estimated from Fish. Stat. Can. 1973.)

	Southwestern Gulf			Northeastern Gulf		
Species	000 Tons	$000	% Value	000 Tons	$000	% Value
Demersal	42	4,300	16	95.7	9,400	57
Cod	19.1			35.0		
Redfish	7.4			54.6		
Small flats	11.0			5.7		
Atlantic halibut	0.1			0.4		
Greenland halibut	0.1			—		
White hake	3.6			—		
Pelagic	46	2,580	9	7.2	3,500	21
Herring	35.1			7.2		
Mackerel	6.8					
Tuna	0.4					
Alewife	3.2					
Anadromous	2.3	1,000	4	0.3	400	3
Smelt	1.8			—		
Eel	0.5			—		
Salmon	0.05			0.3		
Invertebrates	17.8	16,300	59	4.7	3,200	19
Lobster	6.5			0.7		
Crab	7.1			0.1		
Shrimp	0.02			3.5		
Clams	0.9			0.1		
Scallops	2.1			0.3		
Mussels	0.02			—		
Oysters	1.2			—		
Seaweeds[a]	40	3,500				
	50	5,000	15?			
Seals	12,300 for whole Gulf in 1973 value $189,000					

[a]Seaweeds landing statistics not published for 1974 problems re confidentiality for individual firms.

on the Pacific coast. However, the southwestern Gulf of St. Lawrence has a high potential for such development. Atlantic salmon is currently the most important resource with rivers like the Miramichi, Restigouche, and Margaree providing the action. Commercial fishing for this species has been stopped in the Gulf and off Port aux Basques, Nfld., to allow stocks to recover. For Atlantic salmon the recreational fishery and commerical fishery are in more or less direct conflict.

Bluefin tuna fishing has become an important recreational fishery off P.E.I. with a number of charter boats active. At a more mundane level species such as mackerel and cod are providing scope for increasing charter boat activity on the north shore of P.E.I. Provincial governments are encouraging such activities, and expansion of charter boat activities would provide a further base for occupational pluralism.

Northeastern Gulf of St. Lawrence fisheries (Division 4R and S) — Comparison of statistics from Tables 6 and 7 show that numbers of fishermen from Newfoundland have not changed in the 1956–72 period while those from Quebec have increased by about 35%. Fishermen from the Newfoundland and Quebec regions continue to fish using relatively small boats, although in both regions there has been a marked upgrading in vessels being used — the move to longliners in Newfoundland and increase in size of vessels from the Quebec region are examples.

Technology of gear used has improved markedly (Table 6) as shown by the increase in numbers of cod gillnets and trawl lines used by Newfoundland fishermen. In addition, the number of lobster traps recorded in use from the Newfoundland section has increased by about 75% since 1956.

Statistics of landings (Table 5) and those of fishery methods (Tables 6, 8) present some anomalies. Although landings show shrimp as important there are no shrimp trawlers listed. Scallop draggers are also lacking. However, so-called longliners have recently been converted for shrimp trawling and dredging for Iceland scal-

TABLE 6. Comparison of number of fishermen, vessels, and gear used by fishermen located in western Nfld., ICNAF Div. 4R, 1956 and 1972. (From Fish. Stat. Can.)

	1956	1972
Fishermen	2,464	2,500
Vessel type[a]		
Purse seiner	4	5
Longliners > 25 tons	—	14
Longliners < 25 tons	—	79
Boats (row)	458	125
Boats (gas)	879	1,440
Gear type and quantity[a]		
Pelagic	1,529	2,072
Salmon nets	561	688
Cod nets	6	3,512
Cod traps	89	167
Trawl lines	4,592	7,892
Hand lines	1,699	1,589
Lobster traps	128,409	223,935
Cast nets	127	—
Scallop raker	81	—

[a]See text concerning shrimp trawlers and groundfish draggers.

lops. Another outstanding feature is that about 95% of redfish and 25% of cod from Division 4R and 4S are taken by Canadian trawlers, either from ports outside the Gulf or from ports in Gaspé or northern New Brunswick. Meanwhile, with respect to Canadian landings (1974), about 55% of redfish was taken by Canadian trawlers from outside the Gulf.

Landings of major species classes for 1945, 1956, and 1972 in parts of Divisions 4R and 4S are compared in Table 8. There has been significant increase in amount of groundfish landed by local boats from Division 4R but not from Division 4S. Pelagic and estuarial species increased markedly in Division 4R and invertebrates increased substantially in both regions. The increase in invertebrates has been due to a marked increase in landings of shrimp and scallops. Lobster landings actually decreased by about 50–60% despite an increase of about 75% in traps between 1956 and 1972. Another feature is the changes in relative importance of values for the various species groups.

Southwestern Gulf of St. Lawrence fisheries (Division 4T) — As shown in Table 5, fishermen in the southwestern Gulf make use of a large variety of species. Even earlier fisheries (e.g. 1956) landed almost all species now taken. The difference between 1972 and 1956 appears to be in the extent to which various species are exploited (Table 7). In terms of volume landed, pelagic species have increased nearly 5 times and groundfish landings have increased by about 35%. Increases in groundfish landings have resulted mainly from the addition of redfish to the fishery (Table 10). Increased pelagic fish was due to increased herring catches. Although invertebrate landings remained about the same in 1956 and 1972, lobster landings declined about 45%. Volume of invertebrate landings has been maintained by addition of crabs and shrimp beginning about 1968 and increased take of scallops in recent years (Table 10). However, most groundfish and pelagic species in the Gulf have been subject to wide fluctuations as detailed for herring and redfish in Regier and McCracken (1975). Lobsters have been in continuing decline since early in the period shown.

A striking feature of the fishery in the southern Gulf is the relative importance of invertebrates to landed value, slightly over 50% in 1972 (Table 9), despite the decline in volume of lobster landings. Relative monetary importance of groundfish has declined considerably since 1956 and landed value of pelagic and estuarial species has increased from 9 to 16% despite the ban on commercial fishing for salmon. Seaweeds have also increased markedly, both in volume and landed value.

Fisheries for most major species in the Gulf have passed through the development phase and the phase in which accumulated stocks are being fished up (Table 10). Thus cod, redfish, herring, salmon, scallops, and lobsters are dependent on current recruitment. Recent large landings of both herring and redfish have been based on one or two outstanding year-classes as well as application of more advanced technology (purse-seine and midwater trawls). It is not clear whether landings of shrimp and crabs have actually crested or not. However, it seems that practically all species currently marketable are being exploited heavily in the Gulf of St. Lawrence.

Numbers of fishermen from the southern Gulf region apparently declined by about 25% between 1956 and 1972 (Table 11) and, although statistics of effort are not directly comparable, they do show increases in numbers of larger vessels, probably draggers and purse seiners, and a move away from more primitive craft, rowboats and smaller vessels. The number of persons engaged in major fisheries in 1972 shows (a) a high proportion fishing lobsters, (b) a large number fishing groundfish and herring, and (c) the mobility of fishermen between different types of fishing (most likely between lobsters and other types of seasonal fisheries). Amount of gear used in 1956 bears out the emphasis placed on invertebrates within a fisheries milieu where a large number of different species are exploited.

TABLE 7. Comparison of number of fishermen, vessels, gear, and persons engaged in specific fisheries for the north shore of Quebec, ICNAF Div. 4S. (From Fish. Stat. Can.)

	1956		1972	Gear type & quantity[a]		Persons engaged in major fisheries[b]	
Fishermen	1216		1670	Pelagic gillnets	224	Clams	24
				Salmon nets	509	Crabs	26
Vessel type[a]				Smelt nets	24	Groundfish	1301
Draggers	3	>10 tons	4	Weirs	82	Herring	478
Vessels (10–20 tons)	2	<10 tons	1547	Trawl tubs	209	Lobsters	132
Boats (row)	504		209	Hand lines	1216	Mackerel	87
Boats (gas)	527			Lobster traps	3211	Salmon	227
Smacks	41					Scallops	241
						Smelt	47
						Other	433

[a]Statistics of 1956 and 1972 not directly comparable but illustrate major changes.
[b]Persons engaged in more than one fishery are duplicated.

TABLE 8. Comparison of landings by major species groups for 1945, 1956, and 1972 in ports of (A) ICNAF Div. 4R and (B) ICNAF Div. 4S.

	Groundfish	Pelagic, estuarial	Invertebrates	Other	Seals
A) Tons					
1945		not in same form			
1956	4,672	5,897	1,134	317	
1972	8,165	18,144	1,633	45	
% Value					
1945		not in same form			
1956	20	19	60	1	
1972	21	37	41	—	
B) Tons					
1945	6,033	816	24	—	7,258
1956	4,717	544	68	318	
1972	6,078	1,043	771	—	
% Value					
1945	83	17	—		(105)
1956	57	38	4	1	
1972	55	24	19	—	

TABLE 9. Comparison of landings in ports of the southwestern Gulf of St. Lawrence ICNAF Div. 4T in 1956 and 1972.

	1956		1972	
Species type	Metric ton	% Value	Metric ton	% Value
Groundfish	71,215	41	97,523	28
Pelagic & estuarial	26,762	9	128,822	16
Invertebrates	17,237	49	17,690	53
Seaweeds	4,082	1	24,494	3
Other	907	—	—	—
Total	120,203		268,529	
Total value		$18 million		$35 million

TABLE 10. Landings of major species in Gulf of St. Lawrence ports between 1955 and 1974 (in metric tons).

Year	Cod	Redfish	Herring	Salmon	Scallops	Lobster	Shrimp	Crab
1955	41,731	907	50,803	408	45	12,247	—	—
1956	62,596	2,722	37,195	454	91	14,515	—	—
1959	62,596	3,629	27,216	725	45	12,247	—	—
1962	60,782	4,536	36,287	635	45	12,701	—	—
1965	48,081	19,051	48,081	862	499	10,433	—	—
1968	49,442	52,164	144,244	590	998	9,979	91	4,536
1971	43,999	53,071	152,862	272	816	9,072	1,452	5,443
1972	37,195	50,349	77,565	181	907	8,165	1,089	5,443
1973	30,845	56,700	54,432	227	590	8,165	2,132	7,258
1974	26,762	28,577	36,288	227	272	6,804	3,447	7,258

TABLE 11. Comparison of number of fishermen, and statistics for vessels, gear, and persons engaged in specific fisheries for the 4 provinces bordering ICNAF Div. 4T. (From Fish. Stat. Can.)

	1956		1972	Gear[a] type & quantity		Persons[b] engaged in major fisheries	
Fishermen	15,745		11,928	Pelagic gillnets	15,900	Clams	976
				Salmon nets	435	Groundfish	4,355
Vessels[a]				Smelt nets	5,247	Herring	3,518
Draggers	109	>10 tons <35 ft	21	Tubs trawl	5,453	Lobster	8,047
Vessels (20–40 tons)	18	>10 tons >35 ft	1,061	Hand lines	13,745	Mackerel	1,513
Vessels (10–20 tons)	176	<10 tons <25 ft	2,750	Lobster traps	814,000	Oysters	1,359
		<10 tons >25 ft	6,261	Oyster rakes	951	Salmon[c] (1971)	801
Boats (row)	4,197		1,776	Scallop drags	16	Scallops	719
Boats (gas)	3,760					Smelts	1,233
						Other	2,321
						Crabs	58?

[a]Statistics of 1956 and 1972 not directly comparable but illustrate major changes.
[b]Persons engaged in more than one fishery are duplicated.
[c]Commercial salmon fishing has been banned.

SUMMARY

Briefly summarized, a number of pertinent points can be made: (1) fisheries of the Gulf of St. Lawrence are "mature" and most important stocks are being heavily exploited, with catches dependent on current recruitment; (2) the number of sea fishermen from the shores of the Gulf in 1972 included about 33% of those in Canada and just over 40% of those in the Atlantic provinces. Weather and ice conditions limit the fishery to most fishermen for less than 11 months; (3) landings of invertebrates in the Gulf of St. Lawrence are currently, and have been, preeminent in terms of landed value and position they hold in providing fisheries employment; (4) there has been a gradual upgrading of fisheries technology used by Gulf fishermen and this indicates an increased exploitation effort even though numbers of fishermen have declined.

Part II. Past and Present Science Effort

Fisheries Science, Statistical Gathering Mechanisms, and Extension

SCIENCE

Canadian Atlantic fisheries science has never appeared to have been consciously managed around an inshore–offshore seas relationship. Contrary to popular (and often official) opinion, much work done under the Fisheries Research Board (FRB) was short-term research in aid of fishermen and the regulatory agency (Ricker 1975). For instance, until the 1950s the emphasis was on inshore fisheries studies mainly because that appeared to be where the problems lay. Offshore fisheries were in a developing stage and were essentially being kept under a watching brief. Scientists were certainly aware of "overfishing" problems elsewhere (e.g. developments in

the North Sea), and work on trends in fish sizes, ages, and catch-per-effort were aimed at predicting possible effects of more extensive offshore fisheries beginning in Canadian waters. Studies ranged from mapping stocks, determining life histories, estimating size limits, monitoring fish stocks, to some modelling on a single species basis. Formal publication often tended to be a by-product of the main activity. Science management was formally separated from operational planning of the fisheries management agency; it tended to be paternalistic, but ability and hard work were often rewarded in accordance with work performed with less regard for formal publications.

In more recent years member countries of international commissions such as ICNAF became much more active in establishing regulations with respect to mesh size and then setting total allowable catches (TAC) and quotas. Thus, the research effort has become more concerned with single species assessment of the major commercial fin-fish stocks, some of which were seasonally available in inshore areas. As a result, there has been less emphasis in the area of mapping, monitoring, and modelling of inshore invertebrates, and in research on food chain and environmental factors on which multispecies modelling must be based (Parsons 1976). In earlier years FRB carried out much work in exploration for unused or underutilized species, and much work on introduction of new methodology often funded by the Industrial Development Branch (IDB) of Fisheries and Marine Service. Subsequently IDB carried out such work on a cost-sharing basis with the provinces. Important results were obtained but interpretation was often prone to optimism.

The magnitude of the current Fisheries and Marine Service science effort is as follows: of a total \$62.9 million and 2474 man years for the Atlantic coast regions (1975–76), \$31.5 million and 1180 man years are spent on research and development (R and D), including hydrographic surveys and oceanography. More than half of this R and D expenditure and effort is devoted to administrative, ship, and other R and D support. Of this total, \$737,000 and 47.4 man years is devoted to socioeconomic and statistical work.

Social science research has been structured in a quite different way from the natural sciences and is a relatively new activity, but again has never been programmed along offshore–inshore lines. In government, social science research has been almost entirely in applied economics, and usually related to solution of short-term problems and policy issues. There is no social science organization or sustained research being undertaken which is explicitly concerned with fisheries or inshore fisheries. Economists in operational or planning positions are in the Fisheries and Marine services in both headquarters and in the regions. Total expenditure on professional economists comes to about \$1,150,000 annually. Operational social science or policy analysis related to fisheries is also undertaken in several other government departments at federal and provincial levels.

Canadian university work in the social sciences related to fisheries has also been mainly in economics. Research has rarely been directed with respect to the offshore–inshore dichotomy. University economics expertise has occasionally been used to study inshore problems, e.g. Copes (1972). Meanwhile, the "household resettlement" program in Newfoundland helped to stimulate a counterweight school of thought in social sciences at Memorial University. Their emphasis has been on anthropology and sociology with an occasional interdisciplinary link with economics. As a result, Memorial University Institute of Social and Economic Research has probably given Newfoundland an unequalled position in generating knowledge at the microregional or community level. Studies of north shore communities in Quebec by the Department of Anthropology at Laval University, extension activities by the University of St. Francis Xavier, and Memorial University (e.g. the "Fogo Process"), and studies in local government and public administration at the Institute of Public Affairs at Dalhousie University, along with other efforts, also merit attention. This work has been a first step toward articulating values of the rural periphery.

In universities of the Atlantic region there were, in 1973–74, 717 teachers of social science (including social work); in Quebec, 1512. These social scientists are scattered in many departments and there is little structure or focus to their activities in relation to fisheries per se. Even where fisheries projects can be identified such as "A comprehensive management model for the Canadian east coast fisheries" (\$180,000 over 2 years funded by the Department of Supply and Services), now being undertaken by the Institute of Environmental Studies, Dalhousie University, it is difficult to establish whether this is more directly relevant to inshore seas fisheries problems than another project "marginal work world" (\$880,000 over 5 years funded by the Canada Council), being undertaken by the Institute of Public Affairs, Dalhousie University. (This refers to a project entitled "Segmentation, disadvantage, and development: an analysis of the marginal work world, its relationship to the central work

world, and its role in the evolving maritime provinces." In this project the marginal work world "is conceived as marginal in the sense that it is characterized by small labor-intensive firms, each with a preponderance of low income employees. It stands in contrast to the central work world of government service and large capital-intensive strongly unionized industries." Emphasis is on work rather than that of family, community, or welfare unemployment because of its importance in shaping the status, life experiences, and self-concept of the individual person.) (Institute of Public Affairs 1975)

Social science research work is of course carried out on a much broader policy level both in universities and government. Effectiveness of this has recently been questioned (Sewell 1975; Loubser 1975; Dion 1975), but the Institute for Research on Public Policy (Carrothers 1975) in Montreal is a relatively new departure which may help to fill this gap. ("The Conserver Society" project, undertaken by Groupe Associé Montréal/McGill pour l'Etude de l'Avenir (GAMMA) for the Science Council and 11 other Federal agencies, is also worthy of mention.)

Missing at the community level is a coherent approach to acquiring and interpreting information relevant to the social sciences. However, this is a symptom of something far more general. Whether at the national, fisheries sector, or community levels of policy making and policy analysis, with few exceptions there appears to be a lack of focus and underemployment of existing social science research resources. This applies to both government and universities. Outstanding work has in the past occurred more by accident than by design.

Statistical Gathering Mechanisms

Since the early 1950s, with the advent of ICNAF and other international commissions and their increased regulatory role, the statistical gathering apparatus of Fisheries and Marine Service has expanded into an operation which is fairly effective for assessment of offshore activities. Statistics are now compiled by ICNAF subareas and divisions on the east coast and by a domestic system of statistical areas on the west coast.

Despite this increased sophistication, there has been no corresponding increase in effectiveness in picking up information about parameters critical to inshore fisheries, such as age and skill profiles of fishermen and occupational pluralism and the household economy in relation to the total community. This may be because some are not of direct concern to fisheries. For instance, the statistical system can provide manpower and other statistics, more suitable for planning the creation of jobs for people, when the emphasis in less differentiated communities should probably be on getting people to create jobs for themselves. However, there have been some efforts at obtaining this information mainly at provincial government and university levels. The most important effort is probably the Inshore Fishing Earnings Study undertaken by the Prince Edward Island Department of Fisheries (1974) which aims to obtain time series data on the inshore sector. Other studies such as Daneau (1968) for "la Côte Nord du Golfe Saint-Laurent," and Dyke (1968) for a few selected Newfoundland communities, either cover only a small geographical area, or one particular year, or both.

Indeed, one is left with the impression that the statistical system is designed for control from above rather than from below.

Extension

Extension of research results and statistical information to the final clients has varied according to how the research was managed, the nature of the statistical system, and the nature of the client.

In natural sciences there has been little or no formal extension work in relation to the fishermen. In the past when there was an emphasis on inshore fisheries work, individual researchers may have set up their own quite effective de facto networks. More recently, this may have broken down due to emphasis on committee work associated with pressures from domestic and international regulatory mechanisms. Extension work has always been hampered by the absence of any formal organization for this purpose and the absence of representative fishermen's organizations with which researchers and administrators could relate. However, mention should be made of provincial government and university extension programs and fisheries-oriented programs on CBC radio and TV which have at times played a valuable role. (Nova Scotia now has had seven fisheries representatives stationed around the province for just over one year. Although a step in the right direction, this extension program is naturally more in relation to the provincial fisheries department than to research laboratories.)

The fish processors have always been better organized and, due to differing backgrounds, have been in a far better position to understand research findings and act on the knowledge, although even here the record of technological

innovation has been poor. As a result, fish processors have often represented the fishermen. In this case, extension of research results and identification of research priorities were facilitated by means of fish processors' organizations, FRBC and committees, plus leaflets and articles, and technical publications.

Much research has been tailored to enable the fisheries regulatory or management authority to operate more effectively. Extension of research results has appeared to be partially effective. There have been notable examples where management has been unresponsive to research results. As a result it has been suggested by certain scientists that there is an urgent need to develop significantly improved mechanisms for communicating scientific advice to management. There is a need for domestic management institutions to adopt a system of scientific peer review similar to that of ICNAF, so that scientific knowledge is transmitted on the basis of collegial rather than personal opinion.

Extension of biological research results to the general public has mainly been accomplished by publication of annual reports, leaflets aimed at sports fishermen and consumers, radio and TV interviews, etc. Meanwhile, advice to the political level has been either transmitted via bureaucratic channels or directly to the Minister via FRBC, or by means of parliamentary committee, etc.

Although earlier social science studies (in the 1950s and 1960s) involved considerable interaction with fishermen, social scientists have never had sustained contact with fishermen due to their central work locations. Most of their work has been oriented to policy formulation and to statistics gathering. Due to this and the emphasis on economics, most of their relationships have been with the fisheries management body, the political executive, and sometimes with the processors.

State of Knowledge of Natural Resources in Two Selected Areas

Work on the physical environment, stocks, and fisheries off the East coast of Newfoundland and Labrador and Gulf of St. Lawrence has been fairly extensive but there are rather gaping holes and major lapses in continuity. Mapping and monitoring have probably been most continuous for demersal species. The literature is extensive. We intend to consider species and physical features most important to the inshore areas. For the Newfoundland region we will rely heavily on a review by Templeman (1966), and a recent updating by staff of the Biological Station at St. John's, Nfld. (Pinhorn 1976). For some species the most recent research relates to stock assessments reported to ICNAF.

Labrador and East Coast Newfoundland

Templeman (1966) presented a general picture of currents and temperature conditions applicable to southern Labrador and the Newfoundland east coast based on seasonal hydrographic cruises. Most of the seasonal nature of inshore fishing is a result of hydrographic conditions, including ice conditions, and the migration of fish as inshore water temperatures change.

The cod–capelin–mammal complex — Much of the recent research on cod is aimed at estimating maximum sustainable yield (MSY). Nothing particularly new has been added to earlier research results on definition of stocks (Templeman 1966; May 1967), which showed a summer migration inshore related both to water temperature and migration of capelin. However, the latest information suggests that this cod stock does not mix freely throughout the area (ICNAF Redbook 1975). There is no suggestion of change in the inshore–offshore relationship of this cod stock.

The marked decline both in total cod stock and older mature fish in the stock off southern Labrador and east coast Newfoundland is well recognized (ICNAF Redbook 1975). The resulting decline in stock available to the inshore fishery, which is dependent on a postspawning, feeding migration to inshore grounds has also been recorded (ICNAF Redbook 1974). In addition to the decline in mature fish recent prerecruit surveys by the USSR indicate poor recruitment since 1968 (ICNAF Redbook 1975), and more recent data from virtual population analysis suggests that the "good" 1968 year-class was overestimated (ICNAF Redbook 1975). A TAC for this cod stock complex is, therefore, being set in relation to a reestimated MSY.

The relationship between inshore cod migrations and capelin migrations is well recognized (Campbell and Winters 1973), who state: "Capelin are the main prey organism for a great variety of fish, marine mammals and seabirds in the Newfoundland–Labrador area and as such play a vital role in the trophic ecology." They note the inshore migration of cod in pursuit of capelin during June–July and refer to an analysis (Templeman 1965) which indicates that these migrating cod, which have mostly spawned, feed almost entirely on capelin and put on a large proportion of their annual growth at that time. Further, Campbell and Winters (1973) stated that: "The development of an intensive fishery for capelin in the Newfoundland area will un-

doubtedly reduce the biomass of capelin available to its major predators."

This is likely to have two deleterious effects on the inshore fishery: first, there could be a reduction in the abundance of the predators, and second, the predators' distribution and migratory pattern could be affected.

Research on capelin related mainly to inshore spawnings prior to 1972. In 1972 exploratory fishing by Canadians, and exploratory fishing and sonic estimation of capelin stocks carried out by a Norwegian research vessel showed large quantities of capelin offshore. As a follow-up, landings by foreign vessels of 60,000 tons in 1972 off Newfoundland and Labrador increased dramatically to at least 250,000 tons in 1974. A precautionary TAC of about 500,000 tons was recommended for 1976 (ICNAF Redbook 1975). Advice on TAC for capelin has been based mainly on the estimates of surplus unutilized by reduced stocks of cod and seals, plus echo surveys by Norwegian and USSR research vessels.

Stocks of capelin have been crudely estimated in various ways. Campbell and Winters (1973) estimated that annual consumption of capelin on the east coast of Newfoundland and Labrador ranges between 2,200,000 and 3,700,000 tons. This is based on estimates for cod feeding, amounts eaten by harp seals as estimated by Sergeant (1973), and sea birds by Muir, (1973), and even less precise estimates for feeding by other seals, minke whales, dogfish, salmon, etc. More recently an acoustic survey in the fall of 1974 by the USSR gave a minimum estimate of 1.3 million tons biomass for the northern component of the capelin stock (ICNAF Redbook 1975). Estimation of consumption of capelin by existing predator resources compared to the amount that might have been consumed by these predators before they themselves became exploited gave results similar to those of the USSR. However, a consensus of research scientists who reviewed the data was: *"The importance of the interspecific interactions has been emphasized, but at present it is not possible to do more than speculate as to what effect the . . . catches of capelin might have in terms of the abundance and distribution patterns of predators."* (ICNAF Redbook 1975)

Research surveys and population estimates of seals indicate that stocks of this important resource (harp seals are most important) have been overfished for a long time (Templeman 1966), and in recent years stocks appear to have declined rapidly. Catches are currently under quota and in 1971 and 1972 the quota was not reached (ICNAF Statistical Bulletin). Most recently in 1975, estimates of populations by Canadian biologists suggest that a TAC for the fishery should be considerably reduced if stocks are to recover (however, there are major areas of disagreement, particularly in estimates of natural mortality rates).

Despite the importance of this complex to Canadian inshore and offshore fisheries, on the research side we currently rely on the USSR for estimates of prerecruit strength of cod (ICNAF Redbook 1975), and mainly on the USSR and Federal Republic of Germany for research vessel surveys for adult cod (ICNAF Redbook 1975); and on fisheries of foreign countries for information on sizes and ages of cod taken offshore. Similarly we have relied mainly on surveys by the USSR and Norway for direct estimates of quantities and distribution of capelin in offshore waters (Kovalyov and Kudrin 1973; Dragesund and Monstad 1973; Ulltang 1975; Stanek 1975; Gulimov and Kovalev 1975; Serebov et al. 1975). A review of capelin ecology and estimates of surplus yields from predator dynamics have been carried out by Winters (1975). Nobody has attempted to gain knowledge of basic oceanographic variables that influence the food chain, or of the food chain itself at its lower end.

Other demersal species — (a) *American plaice and witch flounder* — Exploratory surveys inshore on the east coast of Newfoundland show that stocks of these species are not large, and this is confirmed from commercial landings by gillnetters (Fisheries and Marine Service documentation).

(b) *Greenland turbot* — Resource surveys showed important stocks of this species in local bays. Further research showed that they migrate offshore and are vulnerable to offshore fishing (Templeman 1966). These stocks make an important contribution to inshore gillnet catches. Recent yield-per-recruit estimates indicate that not more than 30 thousand tons should be taken in 1976 (ICNAF Redbook 1975).

(c) *other groundfish* — Exploratory fishing for groundfish has shown that species such as redfish, grenadiers, etc., are not available to inshore fishermen. Limited stocks of wolffish and lumpfish are available as incidental catches (Templeman 1966).

Pelagic species — (a) *herring* — Early research on herring from the east coast of Newfoundland (Trinity Bay and Bonavista Bay) suggested that stocks are local (Templeman 1966). More recent information tends to confirm this and suggests a yield of about 10–15 million pounds for each bay.

(b) *mackerel* — This species is intermittently present in large numbers on the east coast of Newfoundland with all landings from coastal waters. Templeman (1966) indicated that little research had been carried out in Newfoundland. Mackerel apparently have occurred irregularly when there are large populations off the maritimes and water temperatures are warmer than usual off Newfoundland. Some recent taggings in Newfoundland have shown recoveries to occur off southern New England (Moores et al. 1975).

(c) *bluefin tuna* — Large tuna occur in southeastern Newfoundland in summer and early fall. Though not fished commercially, in some years they support a considerable sports fishery in Conception and Notre Dame bays. Minimal research effort from Newfoundland has been expended on this species.

Invertebrates — (a) *lobsters* — In earlier years the species was extensively studied. On the east coast they are important in Bonavista and Notre Dame bays. They are intensively fished (Templeman 1966), and present level of effort is not needed to take the current catch. Monitoring shows that the fishery is dependent mainly on lobsters which have moulted to legal size between the end of one fishing season and the next. Little research effort for management is currently expended on lobsters — about 1½ (professional) man years annually.

(b) *snow crab* — Templeman (1966) noted potential for this species, and since then considerable exploratory fishing for this species has been carried out and an estimate of potential landings of about 7 million pounds predicted. The species is already being heavily exploited in some areas and recommendations for various methods of control have been made (R. Miller, personal communication).

(c) *shrimp (Pandalus borealis)* — Potential for this species on the east coast is not well known, but exploratory fishing with MV *A. T. Cameron* suggests that a promising area is Hawke Channel off Labrador (Templeman 1966).

(d) *scallops* — Exploratory fishing has shown many small local concentrations of giant scallops in bays of Newfoundland (Squires 1962), which might allow small supplemental local fisheries. This conclusion is borne out by results of surveys by the Marine Sciences Research Laboratory (MSRL) (Fowler and Fletcher 1975).

(e) *Iceland scallops* — This species is widely distributed (Templeman 1966), but knowledge of their commercial abundance on the Newfoundland east coast is limited. Recent shallow-water surveys in southern Labrador (Fletcher and Haggerty 1975), suggests that deepwater surveys for the species should be undertaken, and a recent newspaper report suggests some success in exploratory fishing carried out by the Newfoundland Department of Fisheries.

(f) *squid* — According to Templeman (1966), short-finned squid is the greatest potential molluscan resource. He considers it inevitable that this squid will eventually be used for human food. A fishery would be dependent on a new year-class each year and this, along with the proportion migrating inshore, will probably cause the catch to fluctuate violently. Currently the entire Newfoundland catch is taken close to shore and has reached a maximum for the whole region of about 10,000 tons.

(g) *blue mussels* — Landings of mussels have reached over 100,000 pounds of meats. Intertidal populations are stated to be generally crowded and slow growing, and recent surveys reported by Fletcher and Haggerty (1975) and Fowler and Fletcher (1975) confirm this conclusion for Labrador, but suggest good concentrations in Bonavista Bay. Culture of blue mussels is being attempted with a suspended rope technique by MSRL in conjunction with Fisheries and Marine Service and shows enough promise that a pilot project is being attempted (Scaplen and Fowler 1975).

Other species — Research on other species has not been as extensive, thus, information is less reliable.

Whale fishing is currently banned and most species, except minke and sei whales, appear to be at low levels. The minke whales were often taken inshore.

Sea urchins are widely distributed inshore around Newfoundland. They were abundant in Bonavista Bay and possibly of commercial size (Fowler and Fletcher 1975), but in Labrador they appear to be too small and possibly too scarce for commercial interest (Fletcher et al. 1975). There may also be problems with maturity of gonads which are the edible portion desired.

Seaweed resources are not well documented for the east coast of Newfoundland although several beds of Irish moss were found in Bonavista Bay (Fowler and Fletcher 1975). More detailed surveys are needed to assess standing stocks and productivity of seaweeds in coastal Newfoundland areas.

Conclusion — One is forced to the conclusion that cod will remain the prime source of any

rejuvenation of the resource base for the inshore fishery. Reasonably good exploratory fishing (mapping) and monitoring for many species leads to conclusions that other groundfish species are supplementary and are currently being fished to capacity; pelagic species such as herring are local and do not provide impressive new resources; abundant capelin stocks would probably have to be fished offshore with costly technology; invertebrates such as lobsters and snow crabs are being intensively exploited; many other invertebrates appear to be too scattered or too slow growing to provide more than small, local, supplementary fisheries; much of the salmon take relies on outside production (New Brunswick and Quebec rivers); and that the hunt for seal stocks will have to be rigidly controlled if a future is to be assured.

However, there are some unutilized species which seem to offer potential and are less well mapped. These include Iceland scallops, pink shrimps, short-finned squid, some seaweeds, and possibly echinoderms. Presumably, lack of markets has been a deterrent to research on these forms.

When one considers monitoring and modelling of the cod stock in the area, the problems are urgent if the base for an inshore fishery is to remain viable. The scope of a few problems can be suggested. For example (a) we know that the quota system devised for this stock is based more on sustained yield of total stock than on considerations for the inshore fishery, (b) we do not know that sustained yield would be consistent with the maintenance of a viable inshore fishery, (c) we do know that the current high exploitation has markedly reduced size and age of fish taken, and that recent recruitment has been poor, but we do not know whether reduction in large fish or environmental factors have affected recruitment, (d) we do not know to what extent Canadian ability to participate in the offshore cod fishery should be developed, and (e) an even more complex question for which answers are unavailable is the effect of fishing and environmental factors on the mammal–cod–capelin complex itself, and more important still, its food chain base. In view of our inability to answer these questions it appears that if the inshore fishery is to be maintained, an arbitrary and conservative management regime is the only realistic management approach to the complex. This approach is likely to need such a large safety factor that the prospects for a sizeable offshore operation are significantly reduced.

The possibility of introducing exotic species, such as pink salmon of the Pacific Coast, should be reexamined as an enhancement move. Recent reports indicate that Soviet transplants of Pacific salmon to the Arctic Ocean off Murmansk have been successful.

Gulf of St. Lawrence

Scientific studies in the Gulf of St. Lawrence on physical and biological sides, have been extensive. We intend to deal mainly with research on resources in relation to their management.

Groundfish — (a) *cod* — Migrations and distribution of the adult cod stock from the southwestern Gulf has been well documented by McCracken (1959), Martin and Jean (1964), Jean (1964), and Kohler (1975). Similar documentation for the northeastern Gulf stock migrations has been recorded by Templeman and Fleming (1962) and Wiles and May (1968). Stocks have been studied by Paloheimo and Kohler (1968) and food habits reported by Powles (1958) and Kohler and Fitzgerald (1969). Annual cruises to the southwestern Gulf have provided information on prerecruit year-class strengths. Egg and larval studies of cod and other groundfish have been reported on by Kohler et al. (1974). Recent stock estimates have been provided for ICNAF quotas (Halliday 1972). Most recently a multivariate approach was used to elucidate simultaneous effects of temperature and estimated parent stock biomass on the recruitment mechanism of Gulf cod (Lett et al. 1975a).

(b) *redfish* — A most important species in the northeastern Gulf in recent years has been studied by Steele (1957) and Sandeman (1961). This slow-growing fish has been subject to wide fluctuations in recruitment and the recent large fishery was based on one or two extremely large year-classes. The redfish fishery is one of the few in the Gulf of St. Lawrence currently prosecuted extensively by Canadian vessels operating from nongulf ports. Extreme fluctuations in redfish recruitment may be a relatively common occurrence. The recent redfish "crisis" is an example of a situation where ample warning given by scientists was unheeded by both managers and industry.

(c) *American plaice* — This species has been studied extensively in the southwestern Gulf by Powles (1965; 1969) who outlined its seasonal distribution, growth, feeding habits, and stock size. American plaice are much less important in the northeastern Gulf.

(d) *other groundfish* — various species of lesser importance have received attention in the southern Gulf, e.g. white hake by Nepszy (1968) and

Kohler (1971), winter flounder by McCracken (1963), to describe their distribution, growth, abundance, etc.

Most groundfish stocks have been monitored regularly by collection of statistics of catch, effort, sizes, and ages from the commercial landings.

Pelagic Species — (a) *herring* — Have been studied intermittently, often with major efforts. One was the Atlantic Herring Investigation Committee study reported by Leim et al. (1957) which included information on its biology and distribution related to hydrography. A major disease epidemic in 1955–56 was reported by Sinderman (1958), Tibbo and Graham (1963), and the story of the subsequent extraordinary year-classes of 1958–59 has been recorded by a number of authors, most recently Winters and Hodder (1975). These year-classes have been the major influence on the fishery since the early 1960s. Tagging in the Gulf of St. Lawrence and off southwest Newfoundland has shown a relationship between the Gulf stock and that of southwest Newfoundland (Beckett 1971; Winters 1971). More recently stocks of the Gulf have been assessed by Winters and Hodder (1975), and the interaction of recruitment mechanisms for herring and mackerel with temperature have been analyzed by Lett et al. (1975b).

(b) *mackerel* — This species which is abundant in the Gulf in some years has not been studied as extensively as herring. However, recruitment mechanisms for mackerel and their efforts on other species have been addressed by Lett et al. (1975a) and Winters (1975). Definition of mackerel stocks in the whole northwest Atlantic area is incomplete (ICNAF Redbook 1975), but recaptures of tagged mackerel, released in the Canadian area off the New England coast, suggest some mixing throughout the total stock. Currently these stocks are being considered together in recommending TAC to ICNAF.

(c) *bluefin tuna* — Research in the Gulf on this species has been limited, although some work has recently been reported in Prince Edward Island. Catches have been monitored, dimensions of fish landed have been collected, and early in this sport fishery some large tuna were tagged (these large fish are now valuable so tagging has ceased). Regulation of fishing in the Gulf has been based more on the general picture for bluefin tuna stocks than specific research in the Gulf.

(d) *alewives* — There has been no recent research on this pelagic species.

Anadromous species — (a) *Atlantic salmon* — Is the anadromous species on which research has focused. The Miramichi River, which enters the southwestern Gulf, is considered to be the greatest producing river and much of the research related to salmon has been directed toward pollution problems (mining, pulp mill wastes, DDT spraying) (Sprague et al. 1965; Saunders and Sprague 1967; Elson 1967; Kerswill 1967; Keenleyside 1967), and the reduction of recruits. Development of a salmon fishery off Greenland and recaptures of salmon there from releases in Gulf rivers pointed out the wide dispersal of this species (Saunders et al. 1965; Allen and Saunders 1967) although the large numbers of recaptures of Gulf salmon in Newfoundland fisheries was well known. Much of the recent marine research has been related to fisheries off Greenland, which has been reported in a series of ICES cooperative reports. Salmon fishing was banned off Port au Basques, Nfld., and in the southwestern Gulf in 1972. Subsequent research has related to changes in river runs of salmon and attempts to estimate the extent to which stock are being rebuilt (Turner et al. 1975).

Invertebrates — (a) *lobster* — The most important species to fishermen in the Gulf of St. Lawrence was studied extensively in earlier years. Life history studies included such parameters as moulting, maturity, hatching, larval growth, behavior, and movements of adults (Templeman 1936a, b; 1937). These merged with an extensive series of observations and experiments directed to an understanding of lobster population dynamics, economics, and the effects of the fishery (Wilder 1957, 1969; Rutherford et al. 1967). In a recent documentation by Fisheries and Marine Service (1975) a summary of lobster research covers several pages. It is too extensive to repeat here; however, this summary points out recent changes in research emphasis and parts seem worth quoting even though out of context:

> "At present, about 10 Fisheries and Marine Service scientists with about equal number of support staff are involved wholly or in part with some aspect of lobster research. Half, or possibly more, of this effort is currently directed towards a feasibility study of lobster culture . . . . Some of the current ecological studies and the efforts to assess damage to lobsters and lobster grounds from heavy mobile fishing gear could improve our understanding of lobster stocks and the commercial fishery. At present, however, the only active research directly concerned with the commercial fishery and the factors affecting lobster populations involves the part-time effort of

> one scientist[2] in Newfoundland . . . . The inadequacy of our knowledge of lobster stocks is clearly shown by the drastic but unexplained decline in lobster landings . . . ."

This report could also have emphasized the lack of even minimal monitoring of landings in recent years (D. G. Wilder, personal communication).

Lobster fishing is one of the most regulated on the Atlantic coast, with licenses, seasons, size limits, prohibition for landing of egg-bearing females, and trap limits in some areas. With such a managed fishery and a marked decline in landings from parts of the southwestern Gulf, an evaluation of management and research support would seem to be of high priority. Increased effort for a multi-species approach to invertebrates in Northumberland Strait was implemented in 1975 (J. Caddy, personal communication), but it is not clear whether this will be a long-term effort.

(b) *crabs* — Research on snow crabs (spider) has almost completely lapsed since Watson, who reported on their maturity, mating, egg-laying (1970a) tag recaptures, and movements of adult males (1970b), the queen crab industry in the Atlantic Provinces (Watson and Simpson 1969); and the high rate of exploitation (Watson 1970c). The fishery developed rapidly and there are suggestions that it is currently overexploited. However, monitoring of landings has been insufficient to provide solid answers even about trends.

(c) *shrimp* — Exploration for shrimp was carried out in the late 1950s (Squires 1961), with best results for pink shrimp in the northeast corner of the Gulf.

Possibilities for a commercial fishery were predicted. A fishery developed by 1968 but tends to be confined to a small, highly productive area. More recent surveys by Fisheries and Marine Service Biological Station, St. John's, Nfld., suggests that potential for shrimp extends over a wide area with an estimated potential of at least 2000 tons annually (landings in 1974 were 3500 tons). It is possible that larger vessels than are now used will be required to exploit the full area.

(d) *oysters* — Much research has been devoted to oysters, their culture and the Malpeque disease being the areas of greatest activity. Much early work has been summarized in a bulletin by Medcof (1961). Recent research has continued to expand knowledge of culture methods and to determine the Malpeque disease organism. Current effort on oysters appears to be in science service fields. Main emphasis has been on surveys to determine oyster-growing potential and extent of shellfish stocks in a number of bays and estuaries; stock assessments on major public fisheries; an oyster spat-fall-inventory project; continued development of rearing methods; and extension work in assisting industry (Rowell 1975). Statistics show a landed value of about $500,000 in 1974 and about 1800 people engaged in the oyster fishery. The number of people (six) reporting on oyster field projects in the Research and Development Branch (Maritimes) report for 1975 seems high compared to lack of man power engaged in lobster field projects (as recorded above), if one considers relative value of the fisheries and number of fishermen employed.

(e) *sea scallops* — Earlier exploration found significant quantities of sea scallops in Port au Port Bay, Nfld. (Dickie and Chaisson 1955; Squires 1962), and in parts of the Northumberland Strait (Medcof 1958; Bourne and McIver 1962). Invasion of large boats in Port au Port Bay (Templeman 1966) and in Northumberland Strait seriously depleted stocks. Stocks in Northumberland Strait were also subjected to mass mortalities due to rapid changes in water temperatures (Dickie and Medcof 1963). Recent assessments suggest a small sustainable fishery in Port au Port Bay (around 100,000 pounds of meat per year) and that a fairly substantial fishery can be maintained in Northumberland Strait. However, recent research on the latter stocks has lagged, mainly related to effects of scallop gear on other species. In 1975 a major multispecies study to include scallops was begun (J. Caddy, personal communication).

(f) *Iceland scallops* — A new fishery (1972) for this species has developed in the northeastern Gulf. Currently it is in the "fishing up" stage on a virgin stock and potential and stability of the fishery is not known.

(g) *other invertebrates* — Species such as blue mussels, sea urchins, etc, have potential in harvesting of wild stocks, or for blue mussels a possibility for culture. Various surveys have been carried out to map resources, and research on possible culture of blue mussels has been reported by the Marine Sciences Research Laboratory (MSRL), St. John's, Nfld. Basic research on euphausids (krill) is being carried out using

[2]Since that time, one additional man-year (professional) and more technical support have been added in Newfoundland.

high frequency sonar and more conventional sampling devices (Sameoto 1974) to determine whether there are concentrations large enough to warrant commercial fishing.

Marine plants — Current work on marine plants is moving into a new phase. Since the midsixties the Industrial Development Branch (IDB) has played a lead role in development of the industry, mainly with engineering and technical aspects of drying. In 1974 the program was transferred to the Resource Development Branch (RDB) which is giving priority to Irish moss. The marine plant unit of RDB has reviewed harvesting techniques and productivity of harvested beds; given high priority to development of regulations; begun assessment of mechanical harvesters; and emphasize development of biological information needed to manage the resource (Pringle 1975). The importance of marine plants to productivity of a region has been recognized in studies at St. Margaret's Bay, N.S. (Mann 1972). Effect of mechanical raking on lobster habitat and direct mortality to lobsters has been studied by Scarratt (1972). As a result of the latter drag-raking has been banned around Rustico, P.E.I.

Mammals — Harp, grey, and harbor seals are the most important species and all are competitors with man for fish stocks of the Gulf, although harp seals are used commercially for their pelts.

Current research on grey seals is oriented to assessing a control program carried out in response to complaints about damage to fishing gear. A new technique using ultraviolet light was used in an aerial survey of Gulf harp seal pups in 1974, to estimate numbers of white coat pups (K. Ronald, personal communication). The hunt for harp seals in the Gulf of St. Lawrence is currently banned except for landsmen of the region. Tagging has shown intermixing of the herds in the Gulf and on the Front off Newfoundland, thus earlier remarks about the state of stocks applies. Much nonsite specific research on behavior and physiology of seals is being carried out at Dalhousie and Guelph universities and results will have important applications to knowledge about Gulf of St. Lawrence stocks.

Earlier research (Scott and Fisher 1958) showed the importance of various seals as final hosts for a nematode, the so-called cod worm, which infects the flesh of various demersal fish species.

Other water uses — Due to the increasing effects of land- and water-based activities, the Gulf of St. Lawrence could in the near future go through as profound changes in water quality, nutrients, and biological composition as Lake Erie has in the last 50 years, except that these changes would be on a much larger scale and would probably affect fishery populations in the whole Northwest Atlantic Ocean. The increasing impact of toxic chemicals on freshwater habitats and fisheries (Hamilton 1976; Harvey 1976) is particularly ominous for semienclosed saltwater systems such as the Gulf. Lack of numerical modelling of ocean circulation (Mann 1976a) and the relatively underdeveloped area of chemical oceanography (Mann 1976b) are causes of extreme concern.

In developing the Ocean Resource Management Program for the Gulf, the multiple-use management of the marine resources was stressed. The priority problems were seen to be fisheries, environmental integrity, climate, and the impact from a major development, such as oil and gas. The crux of the project was the ability to indentify and examine interaction between the four problem areas to develop a basis for an overall management regime, and to evaluate benefits to be gained from trade-offs between resource uses. Basic to all this is an understanding of the productivity of the food chain as influenced by changes in the total ecosystem of the Gulf (Parsons 1975).

Although the Ocean Resource Management Program has not been initiated, there has been considerable research activity in the Gulf of St. Lawrence. This includes oceanographic research undertaken at the Bedford Institute of Oceanography; fish and invertebrate species in the Gulf have been described earlier.

Conclusions — There are two major concerns related to knowledge of the fishery resources in the Gulf of St. Lawrence. First, due to the economic importance of invertebrates, particularly lobster in the southwestern Gulf, research and development in support of management should be more related to landed value. Also, within the invertebrate group there is an apparent need for trade-offs with more attention paid to lobsters rather than to oysters. Second, and more important, because the Gulf of St. Lawrence is almost an inland sea and now virtually under complete Canadian jurisdiction with respect to fisheries management, it is urgent that research and development work switch its emphasis from single species stock assessment to work that enables multiple-use and multispecies management. How much protein, and what balance of species can and should be produced in relation to other water uses? This implies knowledge of the total ecosystems and food chains and how these are

affected by environmental factors influenced by marine uses and land-based activities adjacent to the Gulf or within the St. Lawrence River watershed.

We are also forced to conclude that until we have the knowledge to manage the fisheries on a multispecies basis, we shall have to manage in an arbitrary and conservative manner. The consequences of this are either retarded fisheries development or retarded land-based development (due to multiple-use conflicts and the increasing need for environmental impact assessments).

Research Vessel Capacity

Reviewing current Canadian capabilities we seem less than adequately prepared with people or equipment. We are relying heavily in some regions on the science carried out by foreign research vessels for both prerecruit and adult cod surveys. In addition, we have obviously been relying on Norwegian and USSR research vessels for most survey work on offshore capelin. The largest Canadian fisheries research vessel on the Atlantic coast, the *A. T. Cameron*, is now over 16 years old. The next largest, the *E. E. Prince*, although newer, was originally designed as a replacement for an inshore vessel with the expectation that it would have limited winter use in waters close to shore. These two vessels are expected to cover the offshore area plus the Gulf of St. Lawrence. In addition to lack of available time, neither is able to work in winter in the ice off Newfoundland's east coast. The *E. E. Prince* is too small. The *A. T. Cameron*, a basic side trawler, has been provided with a limited stern trawling capability, but this is inadequate for working in ice. According to information reported to ICNAF (Redbook 1975), the *A. T. Cameron* was to be equipped with an echo-integrator by the fall of 1975 for acoustic work on capelin. However, there is no question that the fisheries research fleet is hopelessly inadequate to carry out the necessary work in the Canadian economic zone.

Part III. An Analysis

Scientific Activities and Regional Development

Information gaps identified previously are only marginally different from those for Atlantic Coast shelf-seas fisheries (Regier and McCracken 1975). Importance of science effort for the shelf-seas as a whole can be appreciated in view of the enormous challenge of managing an economic zone at least 200 miles wide around the Atlantic coastline. (This large ocean area is on the same scale as the western plains and B.C., which were acquired by Canada in the 19th century.)

The importance and nature of a science effort sensitive to needs of both inshore and offshore fisheries can only be appreciated if one considers development problems of the Atlantic coast regional economies. In the following policy analysis, it will be seen that the distinction in this geographical area between inshore and offshore fisheries, although largely based on tradition and myth, raises questions about equity and democratic participation and responsibility that are too often ignored in our pursuit of economic efficiency and full utilization. If these questions are raised, what are the implications for the social as well as the natural sciences?

Possibility of Following the Route of Economic Efficiency

The key question is, "Can the regional economies of the Atlantic coast, in particular those of the inshore fisheries communities, follow the conventional route of economic development and industrialization and avoid the negative consequences of industrialization — in particular the low productivity, low relative incomes, and high unemployment to be found in depressed regions?"

It is commonly felt that many inshore fishery communities on the Atlantic coast would not survive if industrialization took its natural course. It is also assumed that urban centers and regional economies of the Atlantic coast would survive and could prosper if proper (i.e. conventional) regional development policies were carried out.

On the basis of the evidence pertaining to fish resources we believe the first assumption is correct. It is the question of how fish and other resources are managed, who makes the decisions about community viability, and what the process of selection is, which we feel is important and not yet adequately answered.

The second assumption seems partially correct. There is little likelihood that any urban centers (with the exception of some single industry mining towns) will die. But it is also unlikely that average incomes and employment in these urban centers will match those of urban centers in richer provinces or regions of Canada unless there are radical changes in policy and action. (The thrust of present regional policy is to concentrate on development opportunities such as energy development in Labrador (and off its shores if oil and gas potential continues to be promising) and transportation gateways in the

Maritimes, along with planned development of each sector of activity. Regional development activities as carried on in each province are an amalgam of large development opportunity projects and sector programs with social development programs (implying adaption to change through encouragement of labor mobility, etc.) following.)

Evidence to suggest this comes not only from the record of regional development performance in Canada (Fig. 5), but also in other developed countries (Anon. 1975b).

Perhaps most significant is that the so-called growth centers of Atlantic coast regions are unlikely to generate enough employment at high wage levels to attract most of the labor from labor surplus inshore fishery communities. This premise has led Copes (1972) to advocate phased depopulation of Newfoundland to mainland areas where there is significant pull from the economy.

Rarely have Atlantic coast regional and fisheries problems been publicly viewed in an all-encompassing manner so that political power, its patterns and dynamics are considered. Brox (1972), Copes (1970), and Gibbons and Voyer (1974) have provided a useful start in this direction. There has been little or no public evidence of any sector planning or action flowing from such a broad policy analysis.

Brox (1972) stated, "It is my conviction that a learned treatise of the fishing industry, which does not deal candidly with the problems involved in the distribution of power among the different interests, is completely useless and in itself a contribution to the maintenance of stagnation. Another criticism which I would like to put forward is that the problem of stagnation and dualism in the province is not fruitfully dealt with in sectoral terms. The province could do with less thinking in terms of industries and more in terms of local communities."

Indeed there is reason to suppose that much of the sector planning and recommendations for action, particularly in fisheries, have not been acted on due to social and political factors in the so-called sociopolitical subsistence system. (In an article "Wanted: A policy for the Newfoundland fishery," APEC (1974) summarized the policy advice stemming from a long line of reports dating back to the early 1950s. The conclusion was that there is enough advice on the shelf. What is now needed is planning and action.) This system has been a Canadian Atlantic coast variety of the power relationships that contribute to the cycle of underdevelopment found in depressed regions of rich countries and in the third world.

Sociopolitical Subsistence System

The sociopolitical subsistence system could be described as a three- or four-cornered "play" or "game" with the following participants manipulating each other: federal government, provincial government, organized interests, e.g. corporations, labor unions, and unorganized interests, e.g. the electorate mainly in rural areas and very often in inshore fishery-based communities.

Each player's actions have been affected by the following circumstances or handicaps that applied to Newfoundland in particular and to other Atlantic coast regions to a varying degree:

1) The international common property nature of marine fish resources, the complex and poorly understood interactions between fish species and their marine environment, and the monopsony powers of different sets of fish buyers at the landed fish stage and at the end-market wholesale levels. These have led to lack of predictability and control, affecting not only behavior of fishermen and dependent communities, but also the processing industry.

2) The social and political characteristics of small fishing villages (e.g. egalitarianism, conflict avoidance, situational leadership, inverse bargaining, etc.). (This is well documented in the Newfoundland Social and Economic Studies carried out by the Institute of Social and Economic Research, Memorial University, Newfoundland.) These had a mutually reinforcing interaction with other sets of handicaps to create a high degree of vulnerability and dependency. The most important characteristic of the communities has been their heterogeneity (Park 1973). Hence, it has been virtually impossible to predict the consequences of any actions initiated from outside the community, thus the common failure of centralized government programs.

3) Political behavior of leaders in the provincial regions (i.e. federal and provincial politicians and civil servants, private corporate management, entrepreneurs, merchants, and labor union executives). Their transactions between each other have often departed from those normally described in economics textbooks (see Gwyn 1968; Noel 1971; Gibbons and Voyer 1974). For instance (a) the indigenous business interests often had substantial control over governments and thus tended to be protected by the granting of monopoly powers and subsidies; (b) through subsidies, loan guarantees, and concessions, international promoters and multinational companies were encouraged to develop the land-based natural and low-cost labor resources of the Atlantic provinces. (Typically, such resource developments have been highly capital intensive

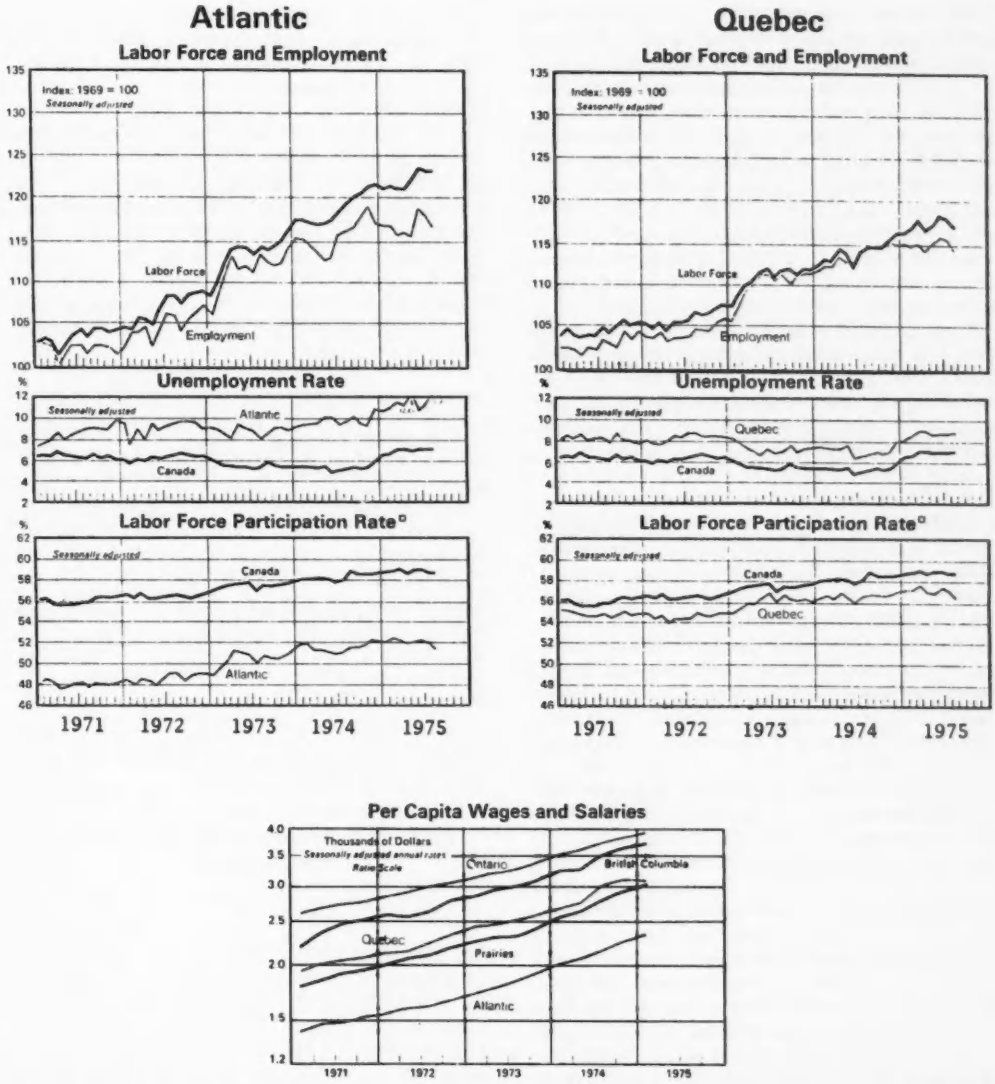

FIG. 5. Labor forces, employment, per capita wages, and salaries for the Atlantic provinces and Quebec. (Source: Canadian Business Trends Regional Indicators, September 1975, Conference Board in Canada)

and the provinces extract little in return by way of real economic development. In the Mezzogiorno (Southern Italy) they have had a similar experience and these petrochemical complexes and other sophisticated hardware have been dubbed "cathedrals in the desert" [Anon. 1975b]). There have also been instances of development based on fishery resources. These outside interests tended to acquire a measure of control over the political parties in the provinces; (c) provincial government members have been alleged to have often traded favors with federal members, especially with the federal cabinet minister from each province (Gwyn 1968); (d) federal and provincial governments traded welfare, infrastructure projects, and handouts for votes from the people or unorganized interests, in particular those from rural areas (see Copes

1970); (There is now evidence to suggest that the unorganized fishermen interests are declining due to unionization. Despite this, there is still likely to be a large residue of unorganized interests who over the long run may lose access to the fish resources due to union exclusion and/or vessel licensing. This is perhaps analogous to the game of "sotto-governo" — one shoe before the vote, and another one afterwards" — (Anon. 1975b) which is played in the Mezzogiorno and in many other areas of the world.) (e) federal and provincial bureaucracies improved their position by facilitating the above transactions.

4) Geographic and economic peripherality. This had been accentuated by internal political, social, and economic fragmentation within the region (see MacPherson 1972). The federal government often failed to understand the problems and its interventions often unintentionally increased them.

5) A high degree of government intervention in and support of the economy. This has increased the area's dependence on bureaucracies which have had no effective accountability to society nor an effective planning capability (Hartle 1976).

The federal government has lubricated this game with cash — in the form of equalization grants, subsidies, development aid, or social security. The provincial governments have bargained for increased jurisdictional or decision-making power or funds. The organized interests have played a strong role in influencing economic and fisheries policy and obtaining protection, and the unorganized interests have been effective in acquiring subsidies and welfare handouts on a customized basis. This has perpetuated a situation characterized by relatively low incomes, high unemployment, low productivity, large and apparently ineffective federal and provincial bureaucracies, weak and government-dependent private sectors, weak or nonexistent regional and local governments, and a general lack of countervailing institutions. In such a situation all participants have been stymied, and most policies thwarted in formulation or execution. The Committee on Federal Licensing Policy and Its Implications for the Newfoundland Fisheries (1974) observed: This (policy of the 1950s and 1960s) encouraged the development of the corporate offshore sector while responding to the difficulties of the inshore/nearshore with well intentioned but largely ineffective ad hoc programs which maintained some fishermen and their communities while abandoning others . . . The long-run result will be to end up with a corporate fishery while presiding over a slow and painful death for the inshore fishery and its communities, punctuated by periodic professions of concern and promises of a new future. Pursuing this route may be politically easier than the first, but it is ultimately irresponsible.

This committee might also have mentioned that the corporate fishing/processing sector also suffered in its inability to develop into a leading and self-sustaining industry. The existence of the groundfish rehabilitation program is ample testimony to all of these failings. (The immediate causes of the groundfish crisis of 1974 were a combination of the following: (a) inroads on resource by foreign fleets; (b) rising costs in harvesting and processing, especially energy costs; (c) softer markets.)

Changing Context

It is necessary to consider the inshore seas fisheries problem and the sociopolitical subsistence system, in the perspective of two major sets of changes taking place: (1) the changing view of industrialization and urbanization, related to questioning the emphasis on material values and individualism; energy costs; the perception of limits to conventional growth; and the need for biological and cultural diversity, balance, order, and stability. Small communities everywhere have been in decline due to industrialization, but there appears to be a new movement to rural communities (Macrae 1976); (2) ocean resources are now ceasing to be an international common property open to anyone.

Alternative Development Strategies for Regional Economy and Inshore Fishing Communities

There are at least three broad approaches that might be taken with respect to the regional economy and inshore fishery communities: (1) continuing contradictory policies and actions; (2) unionism, corporate mergers, more efficient and coordinated government action, and the inevitable power concentration, centralization, and shake-out of "fishless" exfishermen this would entail; and (3) substantial and creative changes.

Continuing Contradictory Policies and Actions

Policy option (1) is that amalgam of contradictory policies and actions encouraging efficiency and inefficiency which emerged during the 1950s and 1960s. It results in a sociopolitical subsistence system as described above and in palliatives which provide a comfortable dependence for inshore fishing communities in the short run. We assume that this policy action option is not desired.

Unionism, Corporate Mergers, More Efficient and Coordinated Government Action

Policy option (2) is the ideal that underlies present fisheries and regional development strategies. Much of the language used in the most recent fisheries policy document (Fisheries and Marine Service 1976) appears to indicate an orientation to policy option number two, although there are some elements of policy option number three in the proposed strategy. As with all policy documents, the actual option followed depends on how it is interpreted and who implements it.

Such policies encourage centralization of economic activities plus "social adjustment" within a region, when the natural tendency is for centralization on a national scale (Kaldor 1975), and for politically powerful but unorganized rural interests to exert pressure for the status quo and redistribution of economic benefits (Copes 1970).

Even if implementable, the consequences of following a similar set of policies in Newfoundland have already been predicted by the Committee on Federal Licensing Policy 1974.

This policy would be for the province over the years to come to move toward a primary fishing industry predominantly owned and managed by vertically integrated corporations, employing trawlers offshore and company-owned or leased longliners to harvest inshore groundfish and shellfish.

Most social science and planning activity has taken place within the context of policy options (1) and (2).

Substantial and Creative Changes

Policy option (3) could be established with the objective of breaking down the sociopolitical subsistence system and reestablishing conditions for creativity and productivity rather than manipulation. But in formulating such policies there must be a reconciliation of short- and long-term plans and action (Select Committee on Inshore Fishery 1975).

Evidently some form of immediate action or incremental change that is creative rather than being another palliative has to take place (Goulet 1971).

Emphasis should, therefore, be on a combination of action, planning, and science support starting at the community level to be carried out in the context of much broader action and further research in the following areas:

a) Economic growth control policies at the center, i.e. in the richer provinces or regions. A policy of central growth control might include a review of present tariff and trade policies which normally favor the center.

b) Decentralization and dispersion of economic and political powers within the rich and poor regions. In particular, control of large corporate powers (i.e. unions, bureaucracies, and private corporations).

c) Federal and provincial tax changes to encourage dispersal of industry across Canada.

d) Creation of incentives for work, productivity, sacrifice, and self-help, through social security reform, particularly in rural areas where living costs are significantly less.

e) Reforms in political party financing, to favor elimination of the pattern of transactive relationships between corporate bodies (including trade unions and private companies) and the politicians.

f) Encouraging community development programs by independent institutions using self-help approaches (rather than help-yourself philosophies of some recent federal programs), to undermine present patterns of transactive relations of unorganized interests with politicians.

g) Reexamining natural resource sector programs. In particular, to explore and provide on a continuous basis all relevant local natural resource information to communities. Perhaps to have the communities contribute to this themselves. To guarantee access to natural resources at the traditional and sustainable level of availability through setting up of property rights to local people or through licenses or quota systems which are administered under local citizen control.

h) Reexamination and redesign of infrastructure and public service programs and their financing suited to rural rather than urban needs.

i) Determine where economies of scale in production are socially desirable, and examine the possibility of promoting equality by applying concepts of situational leadership and periodic evaluation to large organizations. (This could be tried under (b).)

j) Employ advanced planning concepts in government, i.e. (i) have a built-in requirement for adversary planning, so that official political opposition parties would have the financial resources and expertise to criticize and counter-plan; (ii) ensure there is a continuum of planning and action and feedback from the political level to the lowest level in the bureaucracy (normative–strategic and tactical planning); (iii) allow for planning from above and below (transactional planning); (iv) when planning for a sector or program ensure that it is consistent with an

overall systems understanding and design (integral planning span); (v) aim for and achieve full citizen control (integral planning depth). For these suggestions to be put into effect, the size and scale of federal and provincial levels of government would probably have to drop dramatically.

k) Reexamine media and communication policies to encourage a diversity of view points and cultures.

l) If all other policies have failed to enable a community to be viable as far as local people are concerned, there might be provision for remedial relocation or resettlement with adequate counselling and training programs.

These broad policies have been implicitly recognized in the report of the Committee on Federal Licensing (1974) in their third and recommended fisheries policy option: The third option is to make a final and determined effort to establish a more balanced fishery which includes both the offshore trawler effort and a prosperous inshore and nearshore fishery employing fishermen who are independent in reality as well as in name.

The likelihood of such types of policies being accepted and implemented has been minimal until now, largely because everyone has been reasonably well-off and policy option (2) has been credible. Although option (3) remains largely unexplored, it is probably the only feasible alternative solution consistent with maintenance of democratic values. Similar policies are being advocated by a much wider spectrum of interests and are at least under consideration by some governments.

If such policies were implemented, there would still be a possibility of many inshore fishery communities dying; however, the decision-making process would be mostly in the hands of the people affected and they would be less insulated from realistic conditions by subsidies, etc. Such income support as they received would be designed to cushion any drastic change rather than act as an incentive or disincentive to living in a particular community.

Broad social science priorities in relation to policy options (1) and (2) are already established by the present government and other active institutions. Social science priorities at the societal level in relation to policy option (3) are broadly self-evident from the strategy components.

Congruence of Issues

The idea of progress without cost has become discredited by a number of major issues which have come to the fore recently: (1) population growth, (2) natural resource scarcity, (3) pollution and the preservation of the environment, (4) rapid and uncontrolled technological change, (5) lack of effective planning by government and control over it by citizens, (6) discrepancies between developed and underdeveloped countries and between regions in developed countries.

Industrialization is being seen as a process that caters to people's material wants at the expense of other nonmaterial but vital needs (Maslow 1954). It also caters to the wants of some at the expense of other's vital material as well as nonmaterial needs (Goulet 1971). One key paradox is that higher productivity induced by capital–intensive technology and industrialization appears to reduce the opportunities for a sense of individual productivity, considered to be a basic psychological need (Schumacher 1973; Seers 1969; Illich 1973).

There appears to be general agreement in much literature that there is a need for more equality and dispersal of political power, including citizen control of government planning; global systems approaches to planning; encouragement of biological diversity and multiculturism; use of relevant technology for satisfaction of the full range of human needs; more encouragement of individual productivity and creativity (indeed in relation to science this is seen as maintaining scientific objectivity); decentralization of industry and government institutions and jurisdictions; careful controls over large hierarchic organizations, rather than control of society by these organizations; and more local and regional self-sufficiency and self-governing within a global order.

This list is in broad terms similar to that presented earlier in relation to substantial and creative restructuring of Canadian society, to develop the Atlantic coast regional economies and inshore fisheries. Thus it appears that the pragmatic solution for problems of the periphery is in line with a desired model for the developed center, although there are important differences particularly at the community level.

> "Capitalism is not the product of the 15th century's dominant civilisations, but appeared on their fringes. Anti-models are born, and will be born, on the fringes of industrial societies." (Simonnot 1974).

Could not this observation be applied to the Atlantic coast inshore fishing fringe of the Canadian industrial society?

Closer to home, Johnson (1975) remarked that there is a certain congruency in economic terms between issues of population control, non-

renewable resources, pollution, and distribution of growth between developed and less developed countries and regions.

This congruency extends to shorter-term economic problems, e.g. inflation and unemployment. On December 4, 1975, it was reported that 17 Canadian economists signed a letter to the Prime Minister outlining structural changes they considered to be necessary to fight inflation (Chevelayoff 1975). Since then, Prime Minister Pierre Trudeau has called for a new society. Meanwhile in Newfoundland, Premier Frank Moores recently stated; "We are right back to square one . . . we are going to have to build a different kind of economy and a different kind of society." (Gwyn 1975)

Evidently the problem of Atlantic coast inshore fisheries is no less than an extreme example of Canada's major social, political, and economic dilemma (S. McCall, unpublished data), and has to be dealt with not only at the community and sector level, but also at the broad societal level.

Implications of such changes for social science are immense and will involve not only changes in social science, but alterations in attitudes and administrative structures, as well as modifications of present funding mechanisms (Sewell 1975).

Problem of Bringing About Change

The nature of a future social science effort is interrelated with the basic problem of how to bring about change and what the consequences of this action will be for society. Johnson (1975) put the matter succinctly:

> "Does the enlightened policy-maker seek to impose upon his electors the choice he feels must be made; or does he seek to proselytize so as to bring them to recognize the imperatives he perceives; or does he simply respond to the 'political market' — as some economic theorists like to call the political process — and refrain from making the tough choices until they become evident by reason of impending disaster?
>
> "Each of these courses will bring with it, in turn, its own institutional and behavioural result and response. In the larger social, political and economic perspective, in other words — in the larger 'decision-making' model if you will — neither values nor institutional and behavioural forces can be taken as given, as economic theorists and practitioners have tended too often to do. Policy makers, economic policy practitioners and social scientists alike, must recognize that the methods by which choices are made — as between values and in response to institutional forces — will themselves have an impact, not only upon the choice which is made, but also upon the values and the institutional forces themselves."

Unfortunately the problem may be larger still. A commitment to an egalitarian, democratic, and produtive society seems to fly in the face of cyclical patterns in history (Fig. 6), e.g. Kahn and Wiener (1967).

Part IV. Social Science Needs and Community Initiatives

Social Science-Related Activities and Fisheries Resource Management

> "The fishing community at large has but little patience for further 'studies' and for recommendations which would do little and sometimes nothing to alleviate current problems which cause hardships and despair amongst those of our citizens who wrest their living from the sea." (Select Committee on Inshore Fishery Newfoundland 1975)

This statement reflects frustration by those in

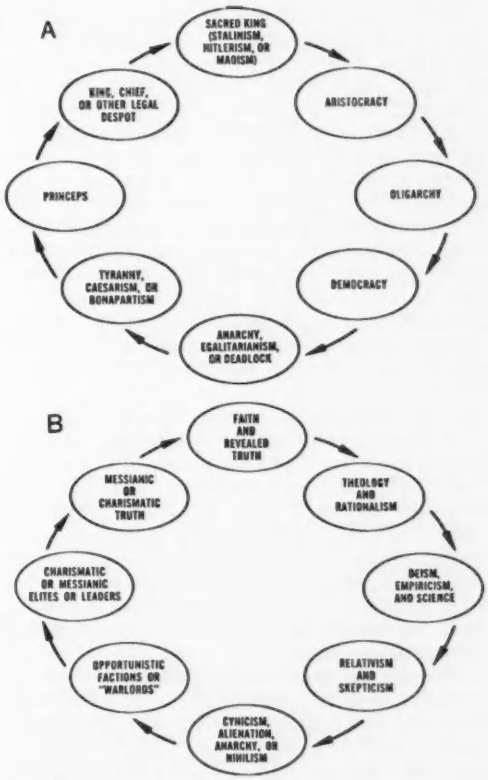

FIG. 6. Recent trends may indicate that we are on the point of moving into a period of anarchy, egalitarianism, or deadlock (A) and into a period of cynicism, alienation, anarchy, or nihilism (B).

or close to the inshore fishery and a partially well-founded skepticism toward use of knowledge. Such skepticism is not so much directed to the natural sciences where there are obvious and critical needs for expansion, but to planning and social sciences where there is a tendency to prescription and little or no implementation followed by deadlock. However, such skepticism is damaging to the natural sciences, as the social sciences could play a valuable role in determining the natural science needs. Also, the generators and purveyors of any type of knowledge are ignored by the ultimate clients. This does not improve the attitude to science of managers who are often too busy to be aware of its potential.

Copes Controversy

Planning ineffectiveness is demonstrated by the fact that Soviet planners have had a far greater impact on the Atlantic coast fishery and in particular the inshore fishery of the northeast coast of Newfoundland and the south coast of Labrador than our own planners. The tendency to prescription and deadlock in social sciences is epitomized by a continuing controversy over the work of Parzival Copes (Evening Telegram 1976) on the Newfoundland Fisheries. (He has also studied other parts of the Atlantic Coast fishery — notably that of P.E.I.) To the casual observer, Copes supporters might appear to fall into the following categories: those at federal and provincial levels who advocate centralization of fisheries and whose power is not threatened by the fishermen and their vote; many economists and engineers; parts of the fish processing industry; and those who believe that persons from outside the region can provide a more objective appraisal of the fishery.

Copes' critics might appear to be governments in power just before elections, and the political opposition; federal and provincial civil servants concerned with the short-term plight of the fishermen and who have a vested interest in subsidy program administration; academics, generally outside the economics and engineering disciplines; parts of the processing industry; those who believe that outsiders are less qualified to work on fisheries problems in the region; and the fishermen's union.

Whether the above categorization is accurate or not, it may not be too oversimplistic to say that Copes and others are advocates of a rather extreme version of policy option (2) — the apparent economic efficiency route. He proposed centralization of fishery activities accompanied by resettlement not only within Newfoundland, but of phased depopulation to the mainland (Copes 1972). His analysis rests on a number of assumptions, the most critical being that Newfoundland has too few natural resources to support its population.

Most opposition to his proposals is either inspired by understandable political and emotional opposition to depopulation of the province and depletion of the subsidy structure, or by romantic identification with the traditional way of life of the outport, i.e. implicit advocates of policy option (1). More thoughtful observers find fault with Copes' assumptions, analysis, prescriptions, and value judgments, and the lack of sufficient exploration of other options and their costs. In particular, past Institute of Social and Economic Research publications (e.g. Brox 1972; Wadel 1969) have pointed in the direction of policy option (3) — substantial and creative change.

In our opinion, Copes is correct in his critique of policy option (1). Within the constraints of policy option (2), which entails implicit trading off of liberty and equality for comfortable dependence or relocation, his analysis and prescriptions are internally consistent, although value-loaded and apparently unrealistic for political reasons. If he were to explore policy option (3), he might find that his assumption about insufficient natural resources is wrong, as natural resource availability and potential is not so much linked to physical but institutional and economic factors. We may be naive in thinking that policy option (3) and its value set is desired by people accustomed to privilege and power, or to the comforts of a welfare state.

In short, Copes and his critics have two different sets of value judgments embedded in their analysis, just as policy options (2) and (3) are based on two different sets of values. (Matthews (1975) and Copes (1975) recently provided some thoughtful observations on the subject of value judgment and factual analysis in policy research related to community resettlement in Newfoundland. Although apparently agreeing with Matthews that there is an ends–means continuum or lack of value freedom in any policy analysis, Copes later added that "my report (Copes 1972) was intended to provide this realistic assessment (of the outport problem) on which value-valid policies could be purposefully structured." We add, does "realism" imply value freedom? We think not.) Meanwhile, option (1) remains the policy of least resistance, and this may sooner or later end in economic disaster. Such is the dilemma for the inshore fisheries and large parts of the Atlantic region.

New Direction for Social Science Related to Fisheries

In view of planning ineffectiveness, and inevitable value biases in the social sciences, it seems that planning and social science related to fisheries should take the following directions if its practitioners are to avoid the label of "enforcers" of the sociopolitical subsistence system: a greater interdisciplinary orientation in planning and social science research; more emphasis on social experimentation and innovation as well as analysis; and provision for bureaucratic accountability, countervailing sources of expertise and "shadow" planning.

Greater interdisciplinary orientation — Referring to an analysis of 62 major advances in the social sciences since 1900, Loubser (1975) stated that interdisciplinary work has been a major intellectual source of contributions. (He also noted that there was not a single Canadian performance among the major advances in the social sciences in this century.)

Fisheries decisions have been made and influenced mainly by natural scientists and engineers, whereas economists have played a subsidiary role. Practitioners from other disciplines in the social sciences have had even less impact. This has reflected a preoccupation with the tactical planning level (MacKenzie 1974).

The incidence of discipline input is likely to vary at each planning level.

Planning level	Discipline emphasis
Values	Philosophy, ethics, history, psychology
Political	Political science, law, sociology, anthropology, ecology, economic history[3]
Strategic	Political economy, public administration, management
Tactical	Mathematical economics, engineering, operations research, mathematics, statistics, natural sciences

However, there would be a need for interdependence and continuity between all levels so that there would be no hard and fast emphasis at any level. At present, it is generally noticeable that events have tended to create a skepticism with respect to the utilitarian ethic that has dominated policy-making for over a century. However, the "softer" social sciences and humanities have not yet replaced it with a dominant or meaningful alternative, although recognition of a hierarchy of needs (Maslow 1954; McCall 1975) and an environmental ethic (Morse 1975) is surely necessary.

Social experimentation and innovation — The social sciences have generally concentrated on research and analysis rather than on communication of results, practical experimentation, and innovation (Saskatchewan Newstart 1970). This is equally true for fisheries (APEC 1974; Select Committee in Inshore Fishery 1975) and in particular inshore fisheries. In view of planning failure social innovations might include rewriting the Fisheries Act (and possibly the BNA Act clauses dealing with fisheries), and legislative and other changes that might make planning more effective. They might also include new marketing and/or fish price-setting mechanisms to remove the much analyzed monopsony powers of fish buyers; experimental fisheries management (Regier and McCracken 1975); and the creation of science networks (Regier and McCracken 1975) to create a focus for interdisciplinary work in the natural and social sciences related to fisheries and ocean resources. Such networks could be centered in Quebec City, Halifax, and St. John's.

Apart from the key area of fish prices and marketing, the most significant innovation at the government level would perhaps be to set up Coastal Zone Commissions generally along the lines suggested by Johnston et al. (1975). A similar proposal for a Maritime Coastal Zone planning Committee to be jointly appointed by the Council of Maritime Premiers and the Federal Government, was made earlier at the Maritimes Coastal Zone Seminar held at Mount Allison University, May 16–18, 1973 (Nova Scotia Resources Council et al. 1973).

According to them, the mandate of the Commission would be:

> "To identify, appraise, and articulate the needs of the coastal zone in each region with a view to influencing policy discussions at all three levels of government that would have an impact on the coastal zone and to gradually create a climate of opinion and practice in which coastal zone management is a reality. Furthermore, it would be the responsibility of the Coastal Zone Commissions to seek to obtain throughout the regions under their jurisdictions a heightened degree of intergovernmental and interagency cooperation in the development and implementation of coastal zone administrative operations."

However, it might be more appropriate to have three rather than the two Commissions suggested

[3]The relevance of the historical approach for obtaining an understanding of inshore fisheries problems has been demonstrated recently by D. Alexander (unpublished data).

by these authors; the first for the Gulf of St. Lawrence with representation from all bordering provinces including Quebec, the second for the northeast coast of Newfoundland and Labrador, and the third for Nova Scotia and the Bay of Fundy. The Gulf of St. Lawrence is the first logical candidate for such institutions.

Social innovations should also be encouraged from nongovernmental sources. For instance, the 40 or more fishermen's organizations plus other interest groups with a stake in inshore fishery communities (e.g. independent processors, regional development associations, etc.) in the Atlantic coast provinces might find it advantageous to form a federation or Inshore/Nearshore Fisheries Council to formulate fisheries and more general policies which they favor, to carry out research, and to lobby governments. There is a lot of merit to a similar proposal for a Newfoundland Inshore/Nearshore Fisheries Council by the Newfoundland Committee on Federal Licensing Policy (1974), but the idea of such a Council being funded by government is questionable. Also, representation of inshore fishermen can only be increased by alignment with a broad range of interest groups on an interprovincial basis. (Such an organization should have objectives which transcend those of individual or pressing issues, e.g. fish price, and whether a fisherman is to be characterized as laborer, businessman, or member of cooperative. Although important, such issues tend to be divisive, and weaken the cause for better fisheries management and utilization systems designed with the needs of the majority of those affected in mind.) Whatever form this organization ever takes, there is a clear need for representation of inshore fishery interests in much the same manner as the Fisheries Council of Canada.

The most effective action to encourage innovation rather than just analysis would probably be to ensure that government decision-makers in fisheries and marine affairs had a social science training in addition to a background in natural sciences and engineering. Above all, this might be accompanied by more bureaucratic accountability and/or size limitation.

Bureaucratic accountability and countervailing sources of expertise — In 1970, 46% of human science activities were conducted in-house (by the federal government); by 1974, this figure had risen to 54%. There was also less money available to universities in 1974 than there was in 1970 while their federal counterparts saw their position greatly improved although on the whole they were not as qualified in terms of academic degrees as social scientists in Canadian universities (Loubser 1975). This picture also seems indicative of what has been happening with respect to social sciences involvement in fisheries. Part of the emphasis on in-house work is perhaps connected with the Lamontagne distinction between curiosity-oriented and mission-oriented research, and recent emphasis on the latter. Loubser (1975) suggested that for social sciences the term "mission-oriented" research be discarded in favor of "manipulation or control-oriented research."

If the major part of in-house social science research is manipulation or control-oriented, then it is important to ensure that society has countervailing sources of expertise in the universities, industry, other independent institutions, and other levels of government. Political opposition parties might also be funded a specific fraction of any government expenditure on a sector or project to carry out their own research. In fairness, some government ministers actively seek an independent opinion; witness the number of government supported semiautonomous boards and councils etc. (e.g. FRBC). (However, FRBC has only one social scientist member.) This need not cost society any more in the case of the fisheries — it could merely mean a reallocation of existing social science resources away from the federal bureaucracy. Coastal Zone Commissions and Inshore/Nearshore Fisheries Council suggested above could also play an important countervailing role. Whatever the countervailing source of expertise, social scientists should scrutinize carefully the relationship between science, government, and industry to ensure that there is neither a return to preindustrial conditions nor a subversion of democracy by large organizations staffed by scientific technocracy (Dion 1975).

Planners and social scientists have all too often been ignored by decision-makers (Gwyn 1976b) and there is need for bureaucratic reform to create incentives for decisions and actions based on planning and for greater accountability (Gwyn 1976a).

Some Specific Study Areas of Inshore Seas Fisheries

Although there is a need for structural and organizational change in the social sciences related to fisheries, the following subjects related to inshore fisheries are in need of exploration (by order of importance):

1) Alternative ocean management regimes for the post-Law of the Sea era, and the social, economic, and legal implications. What legal

and/or institutional mechanism would be appropriate for inshore seas fisheries management and research? Do we need a revision of the Fisheries Act? There is evidently a need for much stronger representation of noncorporate inshore fishery interests vis-à-vis corporate interests. How is this to be accomplished?

2) Alternatives for allocation of access to fishery resources, e.g. vessel licensing policy options and their social and economic impact. Particular attention should be paid to the question of equity as well as economic efficiency, particularly in the case of the cod–capelin–mammal complex off the northeast coast of Newfoundland and the south coast of Labrador. (Meany (1975) has shown that when under a license system the majority of a community is banned from participating in the use of a common property resource, it is not only logical, but equitable that there should be a royalty system which returns to the community some compensation for the loss of this right. Although he was referring to a national or state community, this argument could be extended so that local communities would benefit from royalties in the case of simple license limitation, and also in the case where offshore or foreign fleets are licensed to take stocks that migrate inshore. Would it be completely impractical to suggest that small communities or groups of them on a regional basis have some measure of decision-making power as to whether the economic rent derived locally from inshore fishermen is dissipated in inefficient fishing activity or whether it is used as a source of local public revenue? Although the Fisheries and Marine Service has made some moves in setting up licensing appeal boards and advisory committees, some discussion, if not research, should surely be directed to such a question.)

3) The Gulf of St. Lawrence program with its social science subprogram is an example of a comprehensive approach to research planning fundamental to fisheries management in the post-Law of the Sea period. It represents a step in the direction of emancipating fisheries management from single species crisis orientation to a multispecies systems approach. Important as this program is, it is unlikely to receive recognition and funding as a whole in the absence of suitable inshore fisheries management institutions (recommended for study under 1), and of changes in Research and Development (R and D) funding philosophy. Although not ideal, it is recommended that present Fisheries and Marine Service resources are reallocated to carry out the most important elements of this program in the natural sciences on an incremental basis if this is possible. (For the natural sciences this is second only in importance to the study of the cod–capelin–mammal complex.)

4) The economics of fisheries science funding. It is generally agreed that an economic rent should eventually be derived by the fisheries. However, this rent can only be extracted after the resource is controlled and the fishing industry is viable. This rent might be used in funding fisheries administration and R and D activities of more immediate and/or specific application while the Canadian taxpayer might continue to support R and D of more general and/or less immediate application. This might be a method of ensuring that R and D is carried out at a level consistent with requirements. If there is an immediate need for R and D expansion, this might be funded by the taxpayer on a "loan" basis to be repaid out of future rents.

5) The economics of fish quality control. Can health regulations be separated from quality control for product differentiation? Are there economic ways of improving quality control? Is the Fisheries Inspection system distorting harvesting and processing investment decisions towards larger-scale units as claimed by Brox (1972)?

6) Studies related to strengthening the marketing arrangements and the demand for inshore fishery products. The Canadian Saltfish Corporation appears to have been a successful innovation for inshore fishermen; what other improvements can be made in this vital area? (This is a much-studied area, ripe for innovation. We have included the topic here to underline its importance and the need for feasibility-type studies, some of which have been initiated under the on-going Groundfish Rehabilitation Program.)

7) The economics of energy in fisheries harvesting and processing.

Identifying Community Alternatives

Inshore fishery communities should ideally be able to obtain for themselves full and accurate information about local resource availability and economic potential. Under policy option (3), they would be encouraged to do this in their own idiosyncratic manner without necessarily patterning it on analytical and planning approaches used by middle-class intelligentsia of government or corporate powers.

Resource Availability

We have insufficient knowledge about traditionally exploited species on a multispecies or

food-chain basis to fine-tune management to the needs of inshore fisheries. We also have inadequate local mapping of invertebrates and seaweeds. The first problem requires a sophisticated research approach by large institutional laboratories and the results would be of significance to both inshore and offshore fisheries. However, the second problem of local mapping and monitoring is perhaps amenable to simple data collection, which could be done by local people under professional supervision, on an unpaid and voluntary basis, with small equipment grants and some training. This idea should certainly be investigated when planning coastal zone resources inventories. If it is not practical, then, to insure involvement and responsibility, some means must be found to ensure that local people contribute in some way to mapping and monitoring efforts.

Economic Potential

Analyses of resource availability and economic potential for small communities if carried out at all, are usually carried out by economists working for federal or provincial governments. Their analyses are often based on highly aggregated data and faulty assumptions about people's behavior and preferences (Park 1973). Above all, they normally have no means of assessing local abilities for cooperation and entrepreneurial activity. This type of faulty analysis is carried out because the researcher usually has no effective communication with those who live in the local areas, particularly where there are poorly differentiated communities. Paradoxically, direct communication with the local inhabitants, unless structured properly, can be useless. Communication by outporters with outsiders has often been delegated to a "foolish" leader whose reputation in the community is for foolish talk rather than productive contribution (F. Evans, personal communication).

Park (1973) suggested that:

> "Between the technical scientist and the local fisherman or petty entrepreneur, we want an information broker; that is, a local field worker intermittently in touch with ongoing research in all sectors. He could be a community development worker, a resident social anthropologist, or a survey sociologist."

Others such as J. Lotz (personal communication) are more in favor of a team approach. The field team would consist of three men: one for scanning and screening, a second for organizing people for self-help activities, and a third for research and development.

There is also a need for an extension-type approach between natural scientists and fishermen. Such an approach could to some extent be patterned on agricultural extension approaches in the United States, although it should be borne in mind that fishermen are hunters rather than cultivators.

It appears that such information broker–extention programs are more effective when administered by organizations independent of government. Perhaps the idea of a people's research institute advocated by Coady (1939) and recently reviewed by Lotz (1973) is relevant here.

Tactics will vary according to the degree of differentiation of communities and type of region.

In marginal settlements, communication must largely occur by practical demonstration and experimental testing leading to entrepreneurial and cooperative forms of activity rather than formulation of abstract alternatives for the whole community. (In Newfoundland "show-how is know-how" (F. Evans, personal communication).) Self-help activities should concentrate on acquiring a local economic base that is under their control, i.e. creating jobs for themselves rather than having jobs created for them. (The community development work carried out under ARDA between 1967 and 1970 on the Eastport peninsula in Bonavista Bay, Nfld., and the Antigonish movement in N.S. of the 1920s and 1930s are practical models of what can be accomplished.) Pressure tactics only have creative potential if local people feel they are being hindered unfairly. Exploitation of the cod–capelin–mammal complex by outside interests without due regard to the traditional fisheries, and artificially low fish prices due to monopsony powers of fish buyers are prime examples of this type of hindrance.

In more differentiated communities, where the economic base is more assured and economic activities are on a larger scale (e.g. parts of Nova Scotia), local issues are more concerned with the administration, distribution, and financing of local, regional, provincial, and national public goods and services, and with creating jobs for the local labor force. Information about such issues is more easily conveyed in the mass media. Here there is a need for more sophisticated regional and local planning. To quote Johnston et al. (1975):

> ". . . there is scope for the development of professional services to local authorities, particularly in the regional and local planning fields. Such services, available for reference or on short-term contract, could also provide federal and provincial agencies with improved understanding of local conditions and thus

> reduce the danger of attempting to apply general policies inappropriately in specific situations."

It is also more relevant to use pressure tactics to obtain more control and financial responsibility over local and regional public goods and services; a more equitable distribution of provincial and national public goods; to acquire some degree of industrial democracy; or to develop coastal zone policy (Johnston et al. 1975).

Whatever the approach used, there is a clear need for high caliber fieldworkers and greater participation in government decision-making (McNiven 1974; Johnston et al. 1975) while there are high levels of central government intervention. Benington and Skelton (1973) put the matter very clearly:

> "Community development is a mirror-image of corporate planning, an inductive approach which embodies the notion of intruding into the democratic debate the values and the interests which operate at 'the periphery', to counter the present dominance of governmental decision-making by a narrow range of interests which control 'the centre'."

The immediate aim is to make it easier for people to solve their own problems and become productive. The ultimate aim should be citizen control and financial responsibility involving entrepreneurial and cooperative action in the private sector and strong democratically elected local and regional government.

The cost of free and informed decision-making under policy option (3) requires a measure of risk, sacrifice, and hardship not found under policy options (1) and (2). However, there are intangibles associated with increased self-esteem, belongingness, and self-actualization which may more than compensate for a decline in material well-being (McCall 1975). (It might be argued that the inshore fishery communities — particularly under the terms of the Resettlement Program in Newfoundland — made an informed and free choice. However, there is much evidence to suggest there was lack of counselling about the move and alternative locations (Iverson and Matthews 1968; Copes 1972), including adequate assessment of resource availability and economic potential. Also, the intricate mix of direct and indirect subsidies and social security programs that were available inevitably pulled people in opposite directions. People used available programs shrewdly and this contributed to the apparent ambivalence of attitudes toward resettlement, and thus towards urban versus rural living.)

Conclusions and Recommendations

We have chosen to view science priorities for inshore seas fisheries in the perspective of three broad policy options, each of which has a different value orientation.

The foregoing analysis suggests that irrespective of value set, it is impractical and/or irresponsible in the long-term to impose from above a specific level of Atlantic coast inshore seas fisheries activity by subsidy buttressing or induced centralization. Although practical in the short-run, it is even more irresponsible to try to do both at the same time or to alternate directions in tune with the election cycle.

However, there have to be rules. In accordance with the only untried policy option (substantial and creative change) we recommend, rules must include access limitation, administered in such a way that the people affected have a fair chance of access to the natural resources on which they have been traditionally dependent. Equity to inshore fishermen should be the inviolable constraint to economic efficiency or full utilization, rather than vice versa. This must be accompanied by measures that encourage people to be more independent and productive. This means stimulating entrepreneurial and cooperative activities and self-financed local government, and gradually exposing people to the advantages of open and free competition in the market place both as producers and consumers. This presupposes a willingness on the part of Canadian society in general to commit itself to democracy in its fullest sense and to engage in open and free competition. It entails fundamental change from a consumer society to some sort of conserver society. We realize that it may take a national disaster to elicit the necessary discipline, risk-taking, sacrifice, and hardship required. However, there is already the knowledge and experience for immediate social innovation, especially at the community level. Something can be done.

In the immediate post-Law of the Sea period the responsibilities for science will be enormous under any policy option but far more demanding under policy option (3). The importance of the science effort transcends any relationship to dollars generated in either offshore or inshore fisheries in view of the overriding need to consider equity as a constraint to economic efficiency or to full utilization, and total household, community, and regional economies.

Nothing is possible without a secure natural resource base and the knowledge and wherewithal to manage it. The necessity of a rationalized and expanded natural science effort to allow for a

future expanded and viable Canadian offshore fleet as well as a viable inshore fishery is already recognized by both inshore and offshore interests.

> "It is essential that the scientific effort presently directed towards increasing knowledge of fish populations, of the factors that limit their growth, of their reproductive and recuperative capacities, of their movements and the factors that influence them, should be increased considerably, so that realistic quotas may be set for Canadian fishermen and so that the stocks, upon which inshore fishermen depend, may be protected." (Report of the Conciliation Board 1974)

We are already faced with the problem of allocation of fish stocks among Canadian interests at a time when we still have inadequate knowledge of the resource and the conditions that affect it. Without a stepped-up natural science effort the alternative is an arbitrary and conservative management regime where either or both inshore and offshore fishery interests would suffer. Additional funds for natural science must be sought from redundant operations activities because of changes in management methods within the Fisheries and Marine Service, from user charges obtained from resource rent, and lastly, through increased budgetary estimates (see recommendations below for a reexamination of R and D funding philosophy).

With the exception of additional emphasis on lobsters, local mapping and monitoring, and extension service requirements, the natural science needs for inshore and shelf seas of the Atlantic are practically the same. A transformation of research from single species to multispecies management (Regier and McCracken 1975) and food-chain research along the lines suggested by Parsons (1975) are necessary. This is particularly urgent in coming to grips with the cod–capelin–mammal complex off the northeast coast of Newfoundland and the south coast of Labrador. Another urgent task is to achieve an understanding of the total natural system in the Gulf of St. Lawrence, which is now virtually a Canadian inshore sea affected by both land- and sea-based activities. For this reason we endorse the Gulf of St. Lawrence Program, but have reservations about its ability to attract the necessary funding due to lack of organized support, and of linkage with a purposeful management structure for inshore seas fisheries. (The Fisheries Council of Canada has endorsed the idea of a Gulf of St. Lawrence Program in principle. Such support could be built on if a Coastal Zone Commission for the Gulf of St. Lawrence was set up, and if there was a fishermen's organization (such as an Inshore/Nearshore Fisheries Council) to represent fishermen and associated interests in the Gulf and elsewhere on the Atlantic Coast.) Priorities for at least part of the Gulf of St. Lawrence Program should be assigned from within current federal, provincial, and university sources.

At present, scientific priorities are predominantly determined in relation to demands by ICNAF and the Fisheries and Marine Service with advice mainly from the provinces and the offshore fishing–processing industry; and FRBC with its university and offshore fishing–processing representation. Our study proposes that there is a need to have stronger representation of inshore interests in fisheries and science management. The following measures are recommended:

1) Initiation of a study of management regime alternatives for the Northwest Atlantic fisheries and how to achieve fair representation for inshore fishermen.
2) Fishermen's organizations should be encouraged to form an Inshore/Nearshore Fisheries Council which would represent all inshore fishermen and allied interests on the Atlantic coast and be financed by member's contributions.
3) The idea of Coastal Zone Commissions (as suggested by Johnston et al. 1975), should be further explored and tested on an experimental basis in the Gulf of St. Lawrence.
4) The Fisheries Research Board of Canada should consolidate its position as a science policy advisory body by expanding its interest in the humanities and social sciences, and by giving greater attention to scientific communication and innovation.
5) The offshore–processing representation on the Fisheries Research Board of Canada should be at least matched by inshore fisheries representation.
6) An extension service and information broker–community development system which would provide communications between the natural (and social) scientists and the fishermen, encourage fishermen and people of inshore communities to make a meaningful contribution to map and monitor, and to harvest local resources, especially invertebrates and seaweeds, and above all to stimulate entrepreneurial and cooperative activities (see below).
7) Research and Development funding philosophy should be reexamined in view of the need for larger science effort in a time of government austerity. For instance, it appears that science activities of the future

might fall into three funding categories: (a) local mapping and monitoring, perhaps amenable to inputs and financing (in the long-term on a resource rent basis) by the inshore fishermen and their communities; (b) single species assessment of fish stocks for TAC, a short-term research activity which might eventually be financed (from resource rent) by the fishing industry and foreign fleets; (c) multispecies interactions and environmental research (oceanography) to be undertaken by the federal government and universities and financed by the Canadian taxpayer and rents from foreign fleets.

8) For the natural sciences we endorse the idea of regional networks of expertise and data banks as suggested by Regier and McCracken (1975) to be centered in Quebec City, Halifax, and St. John's. This would help provide a focus for science activity, coordinate work stemming from the three types or levels of science mentioned above, and provide interdisciplinary links with the social sciences (see below). We would also like to repeat the Regier and McCracken (1975) call for an improved research vessel capability.

9) For social sciences and related activities we would like to encourage: (a) more emphasis on social experimentation, communication, and innovation, such as experimental fisheries management suggested by Regier and McCracken (1975), and new forms of marketing and fish price setting mechanisms. Community development to balance corporate planning approaches, and information broker systems are vital. Such approaches should emphasize the use of imagination rather than dispersement of cash, and for this reason should be made by independent organizations that are self-financed; (b) greater interdisciplinary orientation so that social science transcends the tactical planning level; (c) greater bureaucratic accountability so there are greater incentives for plans implemented by managers; (d) countervailing sources of expertise. The idea of funding the official opposition and the universities for independent research as distinct from government-controlled research should be investigated. In addition, representatives from the humanities and the social sciences should have greater representation on FRBC; (e) a greater focus on Atlantic fisheries activities by funding social science in relation to three government–university–industry–consultant regional networks centered in Quebec City, St. John's, and Halifax; (f) recruitment of Fisheries and Marine managers who have a social science as well as biological or engineering training or background; and (g) at a more general level, we would like to encourage broader policy and futures research.

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LETTERS/LETTRES

Comment on Review of *Marine Geotechnology*

BEN RUSSAK, PRESIDENT

Crane, Russak & Company, Inc., New York, N.Y. 10017, USA

RUSSAK, B. 1976. Comment on review of *Marine Geotechnology*. J. Fish. Res. Board Can. 33: 2140.

I am responding to a review of our journal entitled *Marine Geotechnology* which appeared in a recent issue of your journal (Volume 33: 195). It is not often that a small publisher such as ourselves, struggling to meet the demands of the scientific community, and struggling to stay alive at the same time, is referred to as a "robber-baron." I do not need to defend our own name. We are in business to publish ideas, preferably those which are of service to man and his foreseeable environment.

I think, however, that a west coast scientist is on uneasy ground if he criticizes a journal because one half of an issue is devoted to a review of shelf sediments off the eastern coast. After all, there is an east coast, even though it is far away.

I agree with only one statement of your reviewer, which he has inserted into his last sentence, ". . . as long as libraries can afford its price and scientists insist upon its availability, it will be published." That is the whole point: scientists insist upon the journal being published and we will continue to publish it.

The reviewer might well ask himself why commercial firms are now publishing in so many interdisciplinary fields. Professional societies have tended to grow larger and more establishment oriented. They have tended to obscure the demands of newly emerging disciplines. Commercial publishers such as ourselves will continue to fulfill these demands. Furthermore, we will not exact page charges which is something your reviewer has failed to mention.

In any event I would welcome an open discussion of this subject at any time since we feel we are serving the scientific community on the basis of a very low profit, if indeed we are making any profit at all.

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Response of the Reviewer of *Marine Geotechnology*

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Department of Energy, Mines and Resources, Geological Survey of Canada, Vancouver, B.C. V6B 1R4

MILLIMAN, J. D. 1976. Response of the reviewer of *Marine Geotechnology*. J. Fish. Res. Board Can. 33: 2140–2141.

I can understand Mr Russak's displeasure with the tone of my review; if I were in his place, my letter perhaps would have been stronger. The review, although intended to discuss *Marine Geotechnology*, in fact stemmed from a number of years of increased anguish over modern trends in scientific publishing. A similar review might have

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been written about many of the "necessary" journals which have appeared in recent years.

Although I have pointed out the problem (one that an increasing number of scientists are beginning to appreciate), I offer no solution. Clearly the answer lies in both the scientists and publishers as well as those who push the "publish-or-perish" philosophy.

As an aside, I might point out to Mr Russak that I have spent most of my career working on the east coast, studying shelf sediments. "On uneasy ground," I definitely am not!

Sublethal Effects of Toxic Chemicals on Aquatic Animals. *Edited by J. H. Koeman and J. J. T. W. A. Strik. Proceedings of the Swedish–Netherlands Symposium, Wageningen, The Netherlands, Sept. 2–5, 1975. Elsevier Scientific Publishing Co., Amsterdam, Oxford and New York, 1975. vi + 234 p. $24.95 (published in English).*

This volume is a compilation of papers presented at the Swedish–Netherlands Symposium in 1975. The editors point out that the aim of the symposium was to bring together scientists interested in sublethal effects of toxicants on aquatic organisms and promote discussion and information exchange between toxicologists, physiologists, and chemists. Koeman and Strik concluded that those involved benefitted greatly from such a free exchange of views and that such studies could be greatly improved by a multidisciplinary approach.

In essence, the book consists of an assemblage of the 23 papers (many from Swedish or Netherlands scientists) preceded by a table of contents and a short introduction by the editors. The volume is not indexed nor was any attempt made by the editors to synthesize the major findings or identify major new procedures which appear particularly sensitive or useful. Indeed, this would appear to be a volume produced in a rapid manner, as the type for each paper has not been reset but apparently appears as it did in each of the original manuscripts.

In reviewing each of the papers, I found that, in general, they were well written and easily followed, and were not overly wordy. Of course, in an assemblage of papers such as this, one encounters one or two that were poorly done and contain inconclusive or badly controlled experiments. Others, however, are extremely thorough and contain a great deal of useful information. A variety of toxicants are discussed including heavy metals (cadmium, chromium, mercury, lead, zinc), PCBs, detergents, pesticides, herbicides, oil dispersants, kraft mill effluent, phenol, and some contaminated European waters. Approximately one third of the papers deal with marine or estuarine organisms while the remainder deal with freshwater species. Species studied include a variety of fish (eel, perch, flounder, roach, rainbow trout, hagfish, plaice, goldfish), mud crab larvae, polychaetes, *Daphnia*, *Asellus*, *Lymnaea*, and *Artemia*. Many of the toxicant exposure studies use relatively long exposure periods of several weeks and are generally well designed. One general criticism, common to many experiments, was failure to give detailed information on water chemical characteristics or to relate sublethal doseage to acute toxicity test results. Such omissions make comparison of results with those of other tests difficult.

A great many responses to toxicants are described, some of which appear sensitive and useful as sublethal test methods, while others gave disappointing results. Many workers studied blood parameters, ionic balance, histology, enzyme activity, or metabolite biochemistry. Studies with reproductive success, larval species, and osmotic and ionic balance appeared generally useful and sensitive while hematological or diagnostic metabolic tests were nonproductive in some instances. Several papers constitute useful reviews, notably those dealing with tumours in Atlantic eels and possible causes of vertebral damage in fish.

In general, I feel this is a useful book for scientists dealing with sublethal effects of toxicants upon aquatic life and that the volume should be included in a laboratory's library. The research described is certainly current and frequent reference is made to other manuscripts recently published or in press. In addition, the papers provide a useful sampling of the work conducted in many European laboratories concerned with sublethal effects, and indicate the concerns, interests, problems, and progress of those laboratories. Those purchasing the book should be aware that it is essentially a compilation of symposium papers dealing with highly specific subject matter.

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(R109)

Lake Kariba: A Man-Made Tropical Ecosystem in Central Africa. *Edited by E. K. Balon and A. G. Coche. Dr. W. Junk b.v. Publishers, The Hague, 1974. xii + 767 p. $90.*

The need for hydroelectric power has led to the creation of large man-made lakes in many parts of the tropics. Lake Kariba, 4,300 km^2 and 125

m deep, formed when the first Zambezi dam was completed in 1958. It was the first of the recent wave of large new lakes in Africa, and changes studied here as the riverine environment and biota became converted to a lacustrine one are relevant wherever such lakes are being created, and to all who are interested in ecological factors governing the evolution of new plant and animal communities. A limnological study by A. G. Coche (Pt I) describes physical and chemical changes in great detail; Pt II is a study of fish production edited by E. K. Balon.

This book is an important one as it gives the first data on standing crops and biological production from any tropical or subtropical lake. Age and growth studies are notoriously difficult to make at low latitudes. As data in Pt I show, Lake Kariba has an annual overturn, and the regime is seasonal enough for age assessments to be made from growth checks on fish scales and vertebrae. Age determinations made (not without difficulty) on 21 fish species, combined with fish eradication samples from 10 inshore areas, have allowed the computation of fish production. Comparable data are also given for riverine fishes from the floodplain of the Kafue, a nearby tributary of the Middle Zambezi.

Another feature of Pt II is the fascinating study of the replacement of riverine species in the lake by species previously unknown in the Middle Zambezi, mainly Upper Zambezi species. These, it seems, may have been dropping over the Victoria Falls for long ages but failing to become established below these falls until man altered the ecological conditions by creating the lake. Changed spawning conditions appeared to be particularly significant. The lake fish fauna increased from 28 to 41 species. Eels have become abundant despite the dam barrier to upstream migration. The deliberate introduction by man of supplementary *tilapia* species as the lake was forming failed, but a small zooplankton-feeding clupeid introduced from Lake Tanganyika at a later date spread with surprising rapidity. Differences in its biology in the new lake compared with its natural home have, however, affected the potential fishery for this species.

The author/editors are to be congratulated on their great energy in collecting and marshalling an immense number of data, and useful tables give comparative data from other African lakes. It is unfortunate that it is such a bulky and therefore expensive book; much of the information would benefit many people, but few will be able to afford it. The book is bulky mainly because the subjects studied by these two authors are reported in such detail, and many of the photographs of lakeside beauties were surely an unnecessary expense. Despite its bulk, the book is not a complete guide to work on Lake Kariba: readers still have to refer to earlier papers by the authors for many details. An investigation of fish movements made on the Rhodesian side of the lake has been overlooked. A mere half page covers the invertebrate studies on the lake. The tropic relationships of the fishes have not been considered, and no quantitative work appears to have been done on phyto- or zooplankton. Brief mention is made of the floating mat of *Salvinia* water fern which covered up to 21% of the lake surface at one stage. In an epilogue Balon does, however, discuss the ethics of such vast environmental changes and he refers to papers on the resettlement of the displaced human population. References, being "literature cited" rather than a bibliography, contain many citations to work on eastern European rivers and omit some from other tropical man-made lakes (such as Lake Volta).

Lake Kariba comprises four basins which become increasingly lacustrine towards the dam; one third of the water is renewed each year. The upper three basins are now well oxygenated throughout the year. Man-made lakes characteristically pass through three phases. Data for Lake Kariba, the first for a tropical lake, suggest that after an initial productive phase from 1962 to 64, the "trophic depression phase," which sets in when initial nutrients become depleted, continued at least until 1970, 12 years after dam closure. The *Salvinia* mats helped to retain some nutrients in the lake.

Chemical studies suggest that Kariba will remain an oligotrophic lake, relatively deficient in nutrient salts, and is therefore unlikely to be very productive of fish for a tropical lake. In view of this, the estimates for fish production based on age and growth studies seem at first sight surprisingly high. Total production is by far the highest yet recorded, and more than three times that estimated for the Kafue floodplain. Eighty percent of this total is, however, thought to be lost the first year, and the "available production" of 682 kg/ha per yr (or less, if the "area inhabited" by the fish is greater) is perhaps not unreasonable bearing in mind the short life cycles and sustained growth throughout the year of many of the fish. If these Kariba figures are not too high, it bodes well for fish production in other tropical lakes, richer in mineral salts.

Balon redefines many of the terms used in his production studies and the reader must make constant use of the glossary of how terms are used by him. For example, biomasses, far from being synonymous with standing crop, are "interpolated" (computed) "allowing for sampling

bias" to be very much higher, and several forms of production and yield are computed. Echo-sounder surveys indicated that most fish live around the lake in water less than 20 m deep (taken as the "total inhabited area"). Catches varied very much from one sample to another and, as Balon states, most samples proved insufficient for obtaining data within good statistical limits. Little was known about the behavior of individual species. Experience from other African lakes suggests to this reviewer that extrapolation of data from cove-caught samples to total inhabited area could give values that are too high for some species.

Bearing in mind these limitations, mostly discussed by Balon, figures for the various types of production as summarized in the abstract must look too cut and dried. They suggest, however, that the maximum sustained yield is around 40,000 tons/yr for the lake, whereas actual fishing has been exploiting only ca. 3,000 tons/yr. The concluding discussion touches on ways in which more use could be made of the available production. It also provides a useful summary of standing crop and production estimates from many temperate waters for comparison with Lake Kariba. Appendices consider in detail the efficiency of rotenone cove-sampling, the time of annulus formation on scales, a lepidological study, and give tables of data for individual species.

In short, the book is a "must" for consideration by anyone concerned with fish growth and production in tropical waters, and there are good discussions of the limitations of methods used. It is also a book to be mined for facts relevant to many aspects of biology, such as the role of barriers in geographical distribution, and community development and stability.

R. H. LOWE-MCCONNELL

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(R105)

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2220. GILGAN, M. W., AND B. G. BURNS. 1976. The successful induction of molting in the adult male lobster (*Homarus americanus*) with a slow-release form of ecdysterone. Steroids 27: 571–580. (8)

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2226. MAJAK, W., AND R. J. BOSE. 1976. Nitropopanylglucopyranoses in *Coronilla varia*. Phytochemistry 15: 415–417. (2)

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This series includes unpublished preliminary reports and data records not intended for general distribution. They should not be referred to in publications without clearance from the issuing establishment and without clear indication of their manuscript status.

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Journal of the Fisheries Research Board of Canada

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Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

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Journal de l'office des recherches sur les pêcheries du Canada

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Lettres: Opinions sur des sujets exposés dans le *Journal*. Longueur maximale préférable: 500 mots. Le directeur se réserve le droit de raccourcir les lettres et de faire d'autres modifications dans le style du *Journal*.

Dispositions générales

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Il faut éviter les *articles en série*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement (moins de 250 mots) le travail accompli, les points essentiels des connaissances acquises et les principales conclusions. Les résumés paraissent en anglais et en français, le *Journal* veillant à la traduction dans le cas des présentations unilingues.

Le directeur soumet d'ordinaire chaque texte à l'approbation de deux *arbitres* ou plus. Nous encourageons les collaborateurs à suggérer au moins quatre personnes dont les noms pourraient figurer sur la liste des arbitres.

Les *illustrations* doivent être sous forme de reproductions photographiques ne pas dépasser les dimensions d'une page normale et accompagner le texte. Elles ne doivent pas être montées, coupées ni brochées. Les symboles, lettres ou chiffres doivent se détacher avec précision et avoir au moins 1,5 mm de hauter lorsque l'illustration est réduite à la grandeur voulue. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger seulement les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Les tirés à part peuvent être achetés au moment de la publication. Un bon de commande à cet effet accompagne les épreuves; il doit être retourné en même temps que celles-ci, non pas au bureau de la rédaction, mais au Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8, qui se chargera de la facturer. Les frais sont de $40.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

Listes de contrôles pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphs son-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal of the Fisheries Research Board of Canada

Guide for Typists Preparing Copy

Read "Guide for Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send a photographic reproduction (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

Journal de l'office des recherches sur les pêcheries du Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), laissant toujours une marge d'au moins 2,5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les miniscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, ne nom et l'affiliation des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit un reproduction photographique (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir Appendice E). Les noms de revues sont abrégés suivants les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

Call for Papers

Symposium on Environmental Pollutants

An International Symposium on Pathobiology of Environmental Pollutants — Animal Models and Wildlife as Monitors is planned as a 3-day conference on June 1–3, 1977 at the University of Connecticut. This symposium is being co-sponsored by the Northeastern Research Center for Wildlife Diseases, University of Connecticut, Storrs; the Registry of Comparative Pathology, Armed Forces Institute of Pathology, Washington, D.C.; and the Institute of Laboratory Animal Resources, National Research Council, Washington, D.C. The program chairmen are George Migaki, Svend W. Nielsen, and Dante Scarpelli. The purpose is to provide a forum for a free exchange among the 100 participants, of recent information on several groups of pollutants, such as heavy metals, polychlorinated hydrocarbons, and others. It is our intent to have the proceedings published by the National Research Council. Persons interested in presenting papers at this symposium are asked to submit the title and a 100-word abstract by January 1, 1977 to:

George Migaki, D.V.M.
Registry of Comparative Pathology
Armed Forces Institute of Pathology
Washington, D.C. 20306, USA

Invitation à présenter des travaux

À l'occasion du colloque sur les polluants de l'environnement

Au cours de la conférence de trois jours qui aura lieu à l'Université du Connecticut du 1er au 3 juin 1977, il est prévu la tenue d'un colloque international sur la biopathologie des polluants de l'environnement — Contrôle au moyen de la faune et de modèles zoologiques. Ce colloque est parrainé par le *Northeastern Research Center for Wildlife Diseases*, Université du Connecticut, Storrs, le *Registry of Comparative Pathology*, *Armed Forces Institute of Pathology*, Washington, D.C. et l'*Institute of Laboratory Animal Resources, National Research Council*, Washington, D.C. Les réunions seront présidées par George Migaki, Svend W. Nielsen et Dante Scarpelli. Le colloque permettra aux 100 participants d'échanger librement des informations récentes au sujet de plusieurs groupes de polluants, tels que les métaux lourds, les hydrocarbures polychlorés, etc. Nous avons l'intention d'en publier les comptes rendus par le *National Research Council*. Ceux qui désirent faire une communication sont priés d'en soumettre le titre et le résumé (100 mots) au plus tard le 1er janvier 1977 à:

George Migaki, D.V.M.
Registry of Comparative Pathology
Armed Forces Institute of Pathology
Washington, D.C. 20306, USA

3rd Annual Aquatic Toxicity Workshop
"Bioassay Protocols: Standardization and Analysis"

November 2 and 3, 1976
Halifax, Nova Scotia

The aim of the workshop is to continue exchange of technical information and discussion of basic principles relating to all aspects of aquatic toxicity bioassays. This year's workshop will in particular be a forum for discussion on standardization of methodologies, experimental design, and data analysis in bioassays.

Location:
Room H-19, School of Architecture
Nova Scotia Technical College, Halifax, N.S.

Sponsored by:
Toxicity Programs Division
Environmental Services Branch
Environmental Protection Service
Environment Canada
5151 George Street
Halifax, Nova Scotia B3J 1M5

For information write:
Aquatic Toxicity Workshop Committee
at above address

or phone:
E. Pessah, P. G. Wells, or G. F. Westlake
at 902–426–3288, 3289, 6237.

3e Atelier annuel sur la toxicité en milieu aquatique « Protocoles des dosages biologiques: normalisation et analyse »

Les 2 et 3 novembre 1976
Halifax, Nouvelle-Écosse

Cet atelier a pour objet de permettre la poursuite d'échanges d'informations techniques et de discussions sur les principes fondamentaux de l'évaluation de la toxicité en milieu aquatique. Cette année, il portera notamment sur la normalisation des méthodes, les plans d'expériences et l'analyse des données.

Endroit:
Pièce H-19, *School of Architecture*
Nova Scotia Technical College, Halifax,
Nouvelle-Écosse

Parrainé par:
Division des programmes relatifs à l'évaluation de la toxicité
Direction des services de l'environnement
service de la protection de l'environnement
Environnement Canada
5151 Rue George
Halifax, Nouvelle-Écosse, B3J 1M5

Pour de plus amples renseignements, écrire au:
Comité organisateur de l'atelier
à l'adresse donnée ci-dessus

ou téléphoner à:
E. Pessah, P. G. Wells, ou G. F. Westlake aux numéros 902–426–3288, 3289, 6237.

Recent Bulletins/Récents Bulletins

183 Russian–English dictionary for students of fisheries and aquatic biology
W. E. RICKER
(1973, 428 p., cat. no. Fs 94-183; Canada: $7.00, Other countries/Autres pays: $8.40)

184 Freshwater fishes of Canada
W. B. SCOTT AND E. J. CROSSMAN
(1973, 966 p., cat. no. Fs 94-184; Canada: $12.75, Other countries: $15.30)

184F Poissons d'eau douce du Canada
W. B. SCOTT ET E. J. CROSSMAN
(1974, 1026 p., n° de cat. Fs 94-184F; Canada: $12.75, Autres pays: $15.30)

185 Benthic errantiate polychaetes of British Columbia and Washington
KARL BANSE AND KATHARINE D. HOBSON
(1974, 111 p., cat. no. Fs 94-185; Canada: $4.50, Other countries/Autres pays: $5.40)

186 The capelin (*Mallotus villosus*): biology, distribution, exploitation, utilization, and composition
P. M. JANGAARD
(1974, 70 p., cat. no. Fs 94-186; Canada: $3.00, Other countries: $3.60)

186F Le capelan (*Mallotus villosus*): biologie, distribution, exploitation, utilisation et composition
P. M. JANGAARD
(1975, 72 p., n° de cat. Fs 94-186F; Canada: $3.00; Autres pays: $3.60)

187 The lobster fishery of the Maritime Provinces: economic effects of regulations
A. GORDON DEWOLF
(1974, 59 p., cat. no. Fs 94-187; Canada: $3.00, Other countries: $3.60)

187F La pêche du homard dans les Maritimes: conséquences économiques de la réglementation
A. GORDON DEWOLF
(1975, 61 p., n° de cat. Fs 94-187F: Canada: $3.00; Autres pays: $3.60)

Aquaculture in Canada — the practice and the promise
H. R. MACCRIMMON, J. E. STEWART, AND J. R. BRETT
(1974, 84 p., cat. no. Fs 94-188; Canada: $3.75, Other countries: $4.50)

188F L'Aquiculture au Canada — présent en avenir
H. R. MACCRIMMON, J. E. STEWART ET J. R. BRETT
(1975, 88 p., n° de cat. Fs 94-188F; Canada: $3.75; Autres pays: $4.50)

189 Treatment of fish processing plant wastewater
F. G. CLAGGETT AND J. WONG
(1974, 18 p., cat. no. Fs 94-189; Canada: $2.00, Other countries: $2.40)

189F Traitement des eaux usées rejetées par les usines de transformation du poisson
F. G. CLAGGETT ET J. WONG
(1975, 23 p., n° de cat. Fs 94-189F; Canada: $2.00; Autres pays: $2.40)

190 Hydrodynamics and energetics of fish propulsion
PAUL W. WEBB
(1975, 159 p., cat. no. Fs 94-190; Canada: $5.00, Other countries/Autres pays: $6.00)

191 Computation and interpretation of biological statistics of fish populations
W. E. RICKER
(1975, 382 p., cat. no. Fs 94-191; Canada: $8.00, Other countries/Autres pays: $9.60)

192 Catalogue and synopsis of *Caligus*, a genus of Copepoda (Crustacea) parasitic on fishes
L. MARGOLIS, Z. KABATA, AND R. R. PARKER
(1975, 117 p., cat. no. Fs 94-192; Canada: $5.00, Other countries/Autres pays: $6.00)

193 Nearctic and Palaearctic *Heterotrissocladius* (Diptera: Chironomidae)
OLE A. SAETHER
(1975, 67 p., cat. no. Fs 94-193; Canada: $3.50, Other countries/Autres pays: $4.20)

194 Living marine resources of Newfoundland–Labrador: status and potential
A. T. PINHORN
(1976, 64 p., cat. no. Fs 94-194; Canada: $4.00, Other countries/Autres pays: $4.80)

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On peut se procurer les publications ci-dessus, au prix indiqué, en s'adressant directement à:
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Ottawa, Canada K1A 0S9
Payables à l'avance. Faire les chèques et les mandats payables à l'ordre du Receveur général du Canada.

Book Reviews/Comptes rendus

Sublethal effects of toxic chemicals on aquatic animals (J. H. Koeman and J. J. T. W. A. Strik [ed.]), **J. C. Davis**; Lake Kariba: a man-made tropical ecosystem in central Africa (E. K. Balon and A. G. Coche [ed.]), **R. H. Lowe-McConnell** 2142–2144

Coming next month/A paraître le mois prochain 2145
List of recent publications/Liste de récentes publications 2146–2147
Guide for authors and typists/Guide des auteurs et Guide pour les secrétaires d'auteurs *i–iv*

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Announcement/Avis **J. C. Stevenson** 1879

Effects of sand sedimentation on colonization of stream insects **R. J. Luedtke and M. A. Brusven** 1881–1886

Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens* **M. D. Clady** 1887–1893

Ecology of euphausiids in the Gulf of St. Lawrence **F. Berkes** 1894–1905

Selection of artificial spawning sites by the spotfin shiner (*Notropis spilopterus*) **W. F. Gale and C. A. Gale** 1906–1913

Significance of the timing of initial feeding in hatchery rainbow trout, *Salmo gairdneri* **T. K. Twongo and H. R. MacCrimmon** 1914–1921

Molt- and growth-enhancing effects of bilateral eyestalk ablation on juvenile and adult American lobsters (*Homarus americanus*) **J. C. Mauviot and J. D. Castell** 1922–1929

Contribution of gut contents to the concentration and body burden of elements in *Tipula* spp. from a spring-fed stream **J. W. Elwood, S. G. Hildebrand, and J. J. Beauchamp** 1930–1938

Cadmium and zinc toxicity to flagfish, *Jordanella floridae* **R. L. Spehar** 1939–1945

Influence of food competition, predation, and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota **W. A. Swenson and L. L. Smith Jr.** 1946–1954

Community and species responses of Chironomidae (Diptera) to contamination of fresh waters by crude oil and petroleum products, with special reference to the Trail River, Northwest Territories **D. M. Rosenberg and A. P. Wiens** 1955–1963

Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption **D. M. Eggers** 1964–1971

Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*) **J. Janssen** 1972–1975

Direct and indirect effects of oil on ringed seals (*Phoca hispida*) of the Beaufort Sea **J. R. Geraci and T. G. Smith** 1976–1984

Pollution Symposium — 13th Pacific Science Congress **M. Waldichuk [ed.]** 1985–2065

Notes

Basket traps for surveys of a gammarid amphipod, *Anisogammarus confervicolus* (Stimpson), at two British Columbia estuaries **C. D. Levings** 2066–2069

Diel movement of walleye, *Stizostedion vitreum vitreum*, in West Blue Lake, Manitoba, as determined by ultrasonic tracking **J. R. M. Kelso** 2070–2972

Metabolism of single and combined doses of ^{14}C-aldrin and ^{3}H-*p,p'*-DDT by Atlantic salmon (*Salmo salar*) fry **R. F. Addison, M. E. Zinck, and J. R. Leahy** 2073–2076

Improved reagent dispenser for the determination of dissolved oxygen in sea water **C. C. Cunningham, D. D. W. Conrad, J. D. Moffatt, and E. M. Levy** 2076–2078

Seasonal growth rates of mooneye (*Hiodon tergisus*) from the Assiniboine River **C. L. Glenn** 2078–2082

Perspectives

Analysis of large-scale ecological systems **S. R. Kerr and M. W. Neal** 2083–2089

Phytoplankton adaptation to environmental stresses from toxicants, nutrients, and pollutants — a warning **J. G. Stockner and N. J. Antia** 2089–2096

Science for Canada's Atlantic inshore seas fisheries **F. D. McCracken and R. D. S. Macdonald** 2097–2139

Letters/Lettres

Comment on review of *Marine Geotechnology*, **B. Russak**; Response of the reviewer of *Marine Geotechnology*, **J. D. Milliman** 2140–2141

(Continued inside back)